The role of lesser snow geese in positive, degenerative feedback processes resulting in the destruction of salt-marsh swards

by Diane Sheila Srivastava,

Master of Science Degree, Graduate Department of Botany,

University of Toronto, 1993

Abstract

A positive feedback cycle between soil salinity and graminoid growth, triggered by intensive grazing and grubbing by geese, is proposed to account for the loss of graminoid vegetation in an arctic salt marsh (La Pérouse Bay, Manitoba, Canada) based on the results of experimental field studies. Decreases in above-ground biomass, caused by goose herbivory, increase soil salinity. High soil salinities further reduce graminoid growth, both in the salt marsh and under controlled conditions, causing additional decreases in above-ground biomass. Graminoid growth is also reduced by intraspecific competition. The implications of this positive feedback on vegetation dynamics and the size of the goose colony at La Pérouse Bay are discussed.

ACKNOWLEDGEMENTS

I am indebted to my two very capable field assistants, Jennifer Morrow and Jennifer Champion, for doing fieldwork enthusiastically and scrupulously even under physically trying conditions, and for their support and friendship both in the field and in Toronto. Ansgar Schroer was very helpful in constructing a soil press, assisting with the vegetation survey, and setting up computer software. Thanks also to Michelle Watson and other students at La Pérouse Bay who lent a hand.

Bob Jefferies has been a wonderful supervisor, and I thank him for his insightful comments, good humour, and much support and assistance both in the field and in Toronto.

Several friends have been vital in keeping me sane during the preparation of this thesis. In particular, Ritz Chow has been very supportive, and did most of my grocery shopping and cooking in the last frenzy of writing. Deb Wilson kindly lent me a laser printer, and has kept me smiling through it all. As well, my parents provided kilobytes of encouragement via e-mail. Thanks also to the anonymous donor of "Diane's Thesis Survival Kit"!

Dawn Bazely and Alistair Inman have both been very helpful in supplying and discussing a demographic analysis program and modifying it for my data set. This thesis was much improved by discussions with Vic Timmer, Mart Gross, Dawn Bazely, Tony Sinclair and David Hik. ZuZu Gadallah and Don Burrill provided useful statistical advice. Terry Carleton provided computer programs and useful suggestions for the vegetation survey.

Facilities were provided by the Queen's University Tundra Biome Research Station at La Pérouse Bay, the Churchill Northern Studies Center, Dawn Bazely, and Vic Timmer. Funding was provided by NSERC, the Canadian Wildlife Service, and the Department of Indian and Northern Affairs.

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CHAPTER 1: INTRODUCTION

1.1 Opening statement

Rates of change in ecosystems are frequently non-linear (Davis, 1986). It is apparent that some ecosystems can show abrupt and rapid changes in numbers and types of species and in rates of ecosystem processes, often triggered by changes in the abundance of a keystone species (Paine, 1980; Mann, 1982; Bertness, 1984; Power, 1990; Kerbes et al., 1990; Strong, 1992). Strong positive feedback processes often account for such changes in these ecosystems (DeAngelis et al., 1986; Power, 1992). This study examines the role of positive feedback processes in a rapidly changing ecosystem, a degrading arctic salt marsh at La Pérouse Bay, Manitoba, brought about by intensive foraging by a keystone herbivore, the lesser snow goose (*Chen caerulescens caerulescens*).

1.2 Long-term changes in salt-marsh vegetation and a lesser snow goose colony at La Pérouse Bay, Manitoba

The size of the lesser snow goose colony at La Pérouse Bay has increased from 2000 breeding pairs in 1968 (Cooke et al., 1982) to 23,000 breeding pairs at present (R.H. Kerbes, unpublished aerial photographic survey). Other lesser snow goose colonies on the west coast of Hudson Bay have shown similar increases in size (Kerbes et al., 1990). This is not just a local phenomenon. The entire wintering population of lesser snow geese on the Central and Mississippi flyways, of which the La Pérouse Bay birds are a part, has increased from 1.2 million birds in 1973 to almost 2 million birds in recent years (Cooch et al., 1989). This increase in lesser snow goose populations may be caused by changes along the flyways and on the wintering grounds over the last two decades, including a decrease in winter hunting pressure, an increase in the availability of agricultural forage (rice, corn), as well as the establishment of refugia (Reed, 1976; Francis et al., 1992b). At La Pérouse Bay, the increase in colony size has coincided with a long-term decline in clutch size, brood size, gosling growth rates, pre-fledging and post-fledging (first year) gosling survivorship, and in

the size of adult females (Cooch et al., 1989, 1991; Francis et al., 1992a; Williams et al., 1993).

It has been suggested that the loss of high quality summer forage at La Pérouse Bay, in the form of salt-marsh vegetation (Gadallah, 1993), is responsible for declines in fecundity of adults and survivorship of goslings (Cooch et al., 1989, 1991; Francis et al., 1992a; Williams et al., 1993). This is supported by a number of lines of evidence. Gosling pre-fledging survivorship was constant between 1973 and 1988, but decreased exponentially between 1989 and 1992 (Williams et al., 1992, and T. Williams, unpublished data), which coincided with the years of unusually low biomass of salt-marsh vegetation (Fig 1.1). The long-term decline in both gosling pre-fledging survivorship and biomass of salt-marsh vegetation is much greater in the late brood-rearing period than in the early brood-rearing period (Williams et al., 1992). Lastly, substantial post-hatch dispersal of broods to areas with a higher biomass of salt-marsh vegetation (15-65 km away from La Pérouse Bay) has only been observed since 1984 (Cooch et al., 1992). Goslings which have dispersed to such areas have higher growth rates than those which remain at La Pérouse Bay (Cooch et al., 1992).

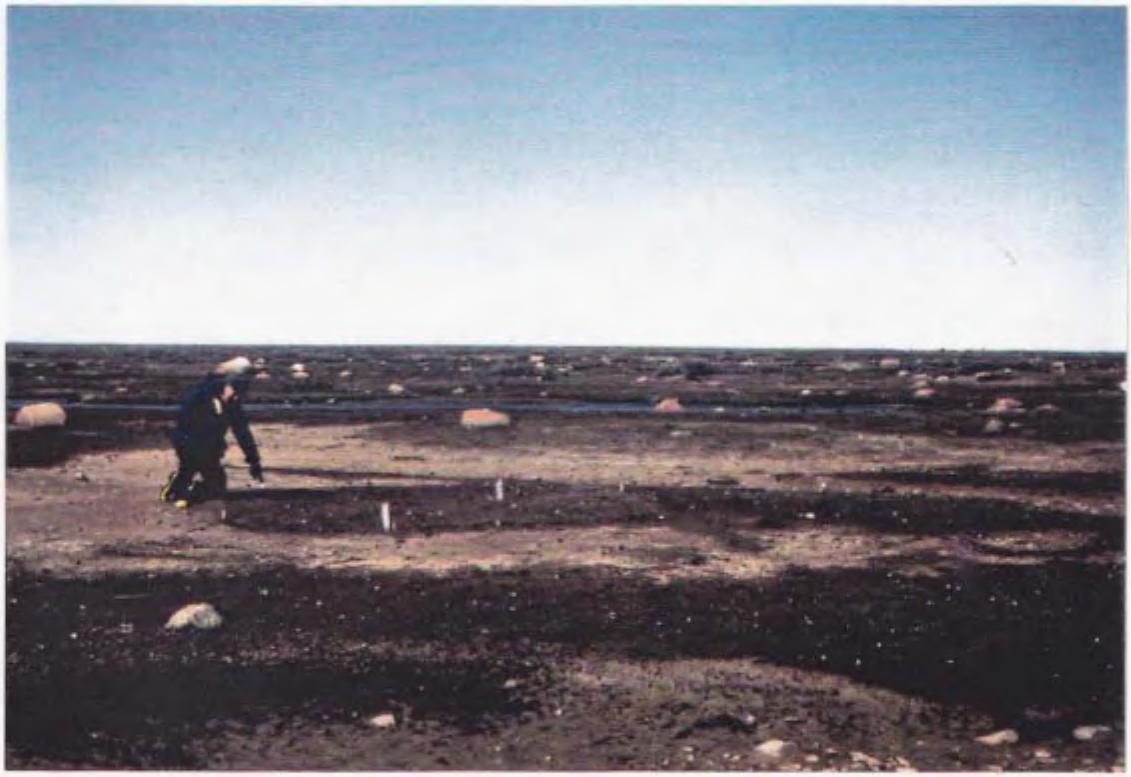
Similarly, it has been suggested that the increase in the size of the lesser snow goose colony at La Pérouse Bay is responsible for the destruction of the salt-marsh vegetation (Jefferies, 1988a,b; Iacobelli and Jefferies, 1991). As described later, snow geese affect vegetation both by grubbing and grazing. Destruction of graminoid swards by grubbing for roots by geese in the spring is widespread (Jefferies 1988b) and increases with spring goose density (including migrants; Jefferies, 1988a). Faecal densities on intact salt-marsh vegetation, which are a measure of grazing pressure, have increased from <1 m^{-2} wk^{-1} to about 10 m^{-2} wk^{-1} between 1982 and 1990 (R.L.Jefferies, unpublished data).

Both the area of salt marsh covered by intact graminoid swards and the biomass of remaining intact swards have decreased substantially over the last decade at La Pérouse Bay, Manitoba (Plates 1.1-1.6). Intact swards decreased by 50% between 1985 and 1989 in

Plates 1.1-1.6. Changes in salt-marsh vegetation from 1982 (1.1, 1.3, 1.5) to 1992 (1.2, 1.4, 1.6) at three sites. Exclosures shown in 1.1 and 1.3 were removed or broken into by geese within a few years of erection. In an inland area of salt marsh (1.1, 1.2), the vegetated area decreased by about 50%, while in more seaward areas of salt marsh, the area vegetated by graminoids decreased by 80% (1.3, 1.4) to 95% (1.5 1.6). The darkest vegetation in 1.4 and 1.6 is *Hippurus tetraphylla*, while the lighter vegetation in 1.4 and 1.6 and almost all vegetation in the other photographs is dominated by graminoids. Notably, the graminoid sward originally exclosed in 1982 (1.1) is still intact in 1992 (1.2), probably due to an increase in elevation caused by exclosure.

1.1

1.2



1.3

1.4

1.5

1.6

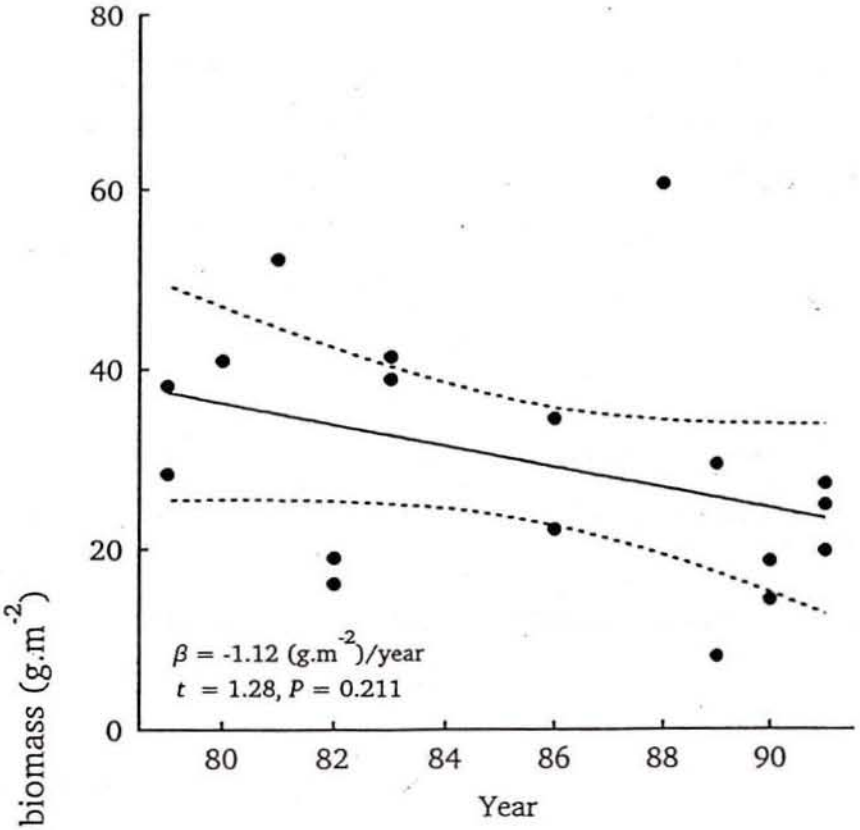
permanent transects (R.L.Jefferies, unpublished data). Between 1979 and 1991, above-ground biomass of the remaining intact swards decreased significantly, from about 50 $g_{dry\ wt}m^{-2}$ to about 25 $g_{dry\ wt}m^{-2}$ (Williams et al., 1993). This decline (Fig 1.1) was not significant in the early brood-rearing period (first 21 days after hatch; usually late June to early July) but was highly significant in the late brood-rearing period (day 22 to day 45 after hatch; Williams et al., 1993). This difference in biomass decline between early and late brood-rearing periods is reflected in biomass change over the season (day 1 to day 45 after hatch). In early years (1979-1982), biomass increased over the season, while in recent years (1988-1991) biomass was constant or declined over the season (Williams et al., 1993). Similar recent decreases in vegetation have been documented for other salt-marshes grazed by lesser snow geese on the west coast of Hudson Bay (Kerbes et al., 1990).

However, it may not be entirely a matter of more geese eating more biomass. In areas inland of the salt-marsh, for example, extensive grubbing by geese around *Salix* bushes has led to exposure of dark peaty soil, causing increases in surface soil temperature, and consequently increases in soil salinity (Iacobelli and Jefferies, 1991). Since high soil salinities cause *Salix* mortality, there has been a progressive and presumably long-term loss of *Salix* bushes from the area (Iacobelli and Jefferies, 1991). Therefore, in addition to directly reducing graminoid biomass, high goose densities may trigger longer-term processes responsible for the decline in salt-marsh graminoid vegetation, as described below.

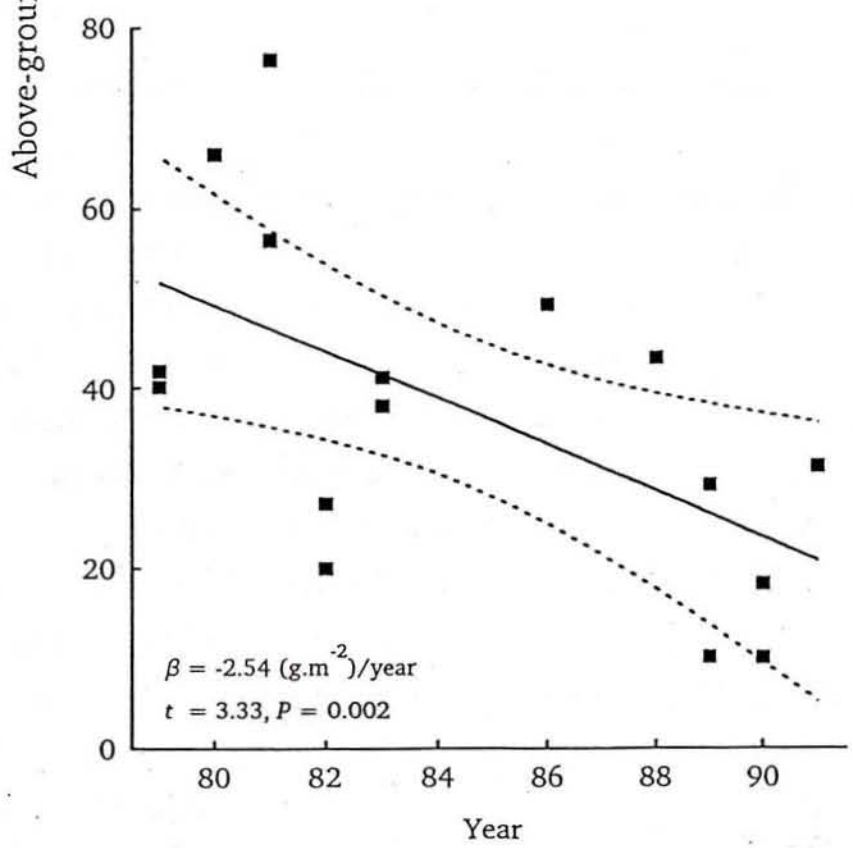
1.3 A positive feedback hypothesis for salt-marsh desertification

A positive feedback model is proposed to account for the progressive degradation of the La Pérouse Bay salt marsh. A positive feedback occurs "when the response of a system to an initial deviation of a system acts to reinforce the direction of change" (DeAngelis et al., 1986). Over-grazing and extensive grubbing by geese is proposed to be the initial deviation or trigger of salt-marsh destruction. The decreased above-ground graminoid biomass in the salt marsh (both standing crop and cover) resulting from such goose activities is hypothesized to result in increased evaporation rates from the salt-marsh soil, producing high soil salinities

Fig. 1.1. Above-ground biomass of intact graminoid swards on the salt marshes of La Pérouse Bay. Data are divided into early post-hatch (<21 days post-hatch) and late post-hatch (>21 days post-hatch) periods. Note that the temporal decline in biomass is both steeper and more significant in the late post-hatch period. From Williams et al., 1993.



Early post-hatch



Late post-hatch

which limit the growth and survival of graminoid plants. Since above-ground biomass is dependent on plant growth and density, above-ground biomass would be reduced, exposing more of the soil surface and causing further increases in soil salinity. In effect, the vegetation is caught in a spiral of destruction. Other processes, such as the formation of thick algal crusts in, and erosion of, unvegetated areas, may also reduce plant growth and survival and so contribute to this positive feedback cycle.

The actions of snow geese act as a trigger of this positive feedback cycle, but are not necessary for further degradation, at least over the short-term.

Validation of this positive-feedback between soil salinity and graminoid biomass requires:

1) Soil salinity to be inversely related to graminoid biomass (Chapter 4)
2) Graminoid growth to be inversely related to soil salinity (Chapter 5)

Supporting evidence for the positive feedback hypotheses would include:

3) An inverse relationship between surface evaporation rates and graminoid biomass (Chapter 4)
4) Carry-over of either biomass or salinity conditions between years (otherwise the positive feedback would not result in progressive destruction of the salt marsh over several years independent of prevailing goose densities; Chapter 2)
5) Similarities in the poor growth of graminoids under saline conditions in the salt marsh with known growth responses of graminoids to salinity (otherwise other soil conditions correlated with soil salinity may be the prime cause of decreased graminoid growth in the salt-marsh; Chapter 6)
6) Inability of other species to colonize unvegetated areas from which graminoids have been removed (otherwise above-ground biomass may not decrease but just change in species composition; Chapter 3)

Such a positive feedback cycle indicated by the above lines of evidence would be consistent with the observed decline in biomass in the late but not early brood-rearing periods discussed earlier. Air temperatures (see below) are higher in the late brood-rearing period and so, presumably, are evaporation rates and hence soil salinity. The positive feedback between soil salinity and plant growth may therefore be stronger in the late brood-rearing period, resulting in a long-term decline in biomass in the late but not early brood-rearing period. Specifically, it is predicted that:

7) Evaporation and soil salinity are higher in warm periods of the season (Chapter 4)
8) The inverse relationship between soil salinity and graminoid biomass is greater in the late brood-rearing period (July 10 to August 4, 1991; July 21 to August 14, 1992) than earlier periods (Chapter 4)

The above eight hypotheses are examined in detail in the remainder of this thesis (as indicated in brackets).

Similar positive feedbacks between soil salinity and plant growth have been proposed to explain *Salix* dieback in more inland areas around La Pérouse Bay (Iacobelli and Jefferies, 1991), poor growth of *Juncus gerardi* in a New England salt-marsh (Bertness, 1991), and pond formation in *Puccinellia phryganodes-Carex subspathacea* vegetation (Mason, 1981).

1.4 Study site location and soils

La Pérouse Bay (58°04'N, 94°03'W) is on the western coast of Hudson Bay, 25 km east of Churchill, Manitoba. The shores of La Pérouse Bay constitute part of the Hudson Bay Lowlands, described by Glooschenko and Martini (1978) as a "vast, flat, featureless plain on the west coast of James and Hudson Bays occupying some 324,000 km^2". The Hudson Bay Lowlands were originally submerged under the Tyrell Sea, but isostatic uplift following deglaciation (7400-8000 years ago) has led to emergence of these areas above sea level. Present rates of isostatic uplift are estimated at 0.5 to 1.2 cm yr^{-1} (Andrews, 1970, 1973). As

a consequence, much of the upper sediments of the Lowlands are underlain by a thick layer of grey, slightly fossiliferous, marine clay deposited in the Tyrell Sea (Glooschenko and Martini, 1978). Bedrock in the Lowlands is of Palaeozoic origin, and consists largely of flat-lying limestone, dolomite, shale and sandstone (Glooschenko, 1980a).

Salt marshes are common on both east and west coasts of Hudson and James Bays (Glooschenko and Martini, 1978; Glooschenko, 1980 a,b; Dignard et al., 1991). The soils of salt marshes of the Hudson Bay Lowlands have been classified as mineral regosols (Glooschenko and Martini, 1978). In particular, soils of salt marshes surrounding La Pérouse Bay were classified as regosolic static cryosols by Wilson (1993). At La Pérouse Bay, between 0 and 10 cm of light brown silty sediments cover the marine clay in the salt marsh (Chapter 3), and alternating bands of light and dark (rich in organic material) sediment are often visible, perhaps reflecting annual tidal influences (Wilson, 1993). The pH of the upper four centimeters of soil is 7.8-8.0 (n=15, June 1, 1991).

The treeline is about 50 km south of La Pérouse Bay and touches the nearby town of Churchill, Manitoba. In terms of vegetation, therefore, Churchill is often represented as being a transition zone between the low arctic and forest-tundra biomes (eg., Polunin, 1951) but different authors have classified Churchill as either subarctic or arctic when climatic criteria are also taken in account (reviewed in Ritchie, 1956; Sage, 1986).

1.5 Graminoid species

The salt marshes at La Pérouse Bay are dominated by two graminoids, a grass, *Puccinellia phryganodes*(Trin.) Scribn. and Merr., and a sedge, *Carex subspathacea* Wormskj. (nomenclature follows Porsild and Cody, 1980). Swards mainly composed of these two species are henceforth referred to as *Puccinellia-Carex* swards. Dicotyledonous species are more minor components of *Puccinellia-Carex* swards and are described in Chapter 3. Aquatic and more inland plant communities of the salt marsh are also described in detail in Chapter 3.

Both *Puccinellia phryganodes* and *Carex subspathacea* have circumpolar distributions, with *P. phryganodes* being the only circumpolar member of its genus (Porsild, 1957; Hultén, 1962; Porsild and Cody, 1980). *P. phryganodes* appears to be continuous in distribution around Hudson and James Bays, with James Bay (53° N) representing its southward limit in North America (Dore and MacNeil, 1980). Both species are restricted to coastal salt flats (Porsild, 1957), and at La Pérouse Bay are only c. 2 cm tall under grazed conditions.

Puccinellia phryganodes forms extensive swards of often monospecific vegetation at La Pérouse Bay, as elsewhere (Polunin, 1959; Dore and MacNeil, 1980). This is the result of extensive stoloniferous growth. Although stolons are reported to be extra-axillary (Polunin, 1959; Dore and MacNeil, 1980), axillary shoots are most commonly observed at La Pérouse Bay. Shoot production is iterative (Bazely and Jefferies, 1989) with secondary axillary shoots rarely forming except under favourable conditions. Flowering at La Pérouse Bay is infrequent and occurs mainly in dense, ungrazed swards although profuse flowering was reported 15 years earlier (Jefferies et al., 1979). Differences in flowering frequency over this time period may reflect increased grazing pressure. In any case, seed set has never been observed (Jefferies and Gottlieb, 1983, and references therein) and the grass is a sterile triploid in North America (Bowden, 1961; Sadul, 1987). Given the asexual nature of this grass, there is a surprisingly high amount of genetic variability both within and between populations in the Canadian Arctic (Jefferies and Gottlieb, 1983; Sadul, 1987).

Carex subspathacea also forms large swards at La Pérouse Bay, due to extensive rhizomatous growth. Kotanen and Jefferies (1987) describe its growth habitat at La Pérouse Bay as a cluster of tillers, joined underground, with the tillers emerging about 0.5 cm apart, and the clusters being joined by rhizomes ca. 10 cm in length. As in *P. phryganodes*, flowering is infrequent and seed has not been found at La Pérouse Bay (Chou et al., 1992) but both flowering and seed set are reported at other locations (Polunin, 1959).

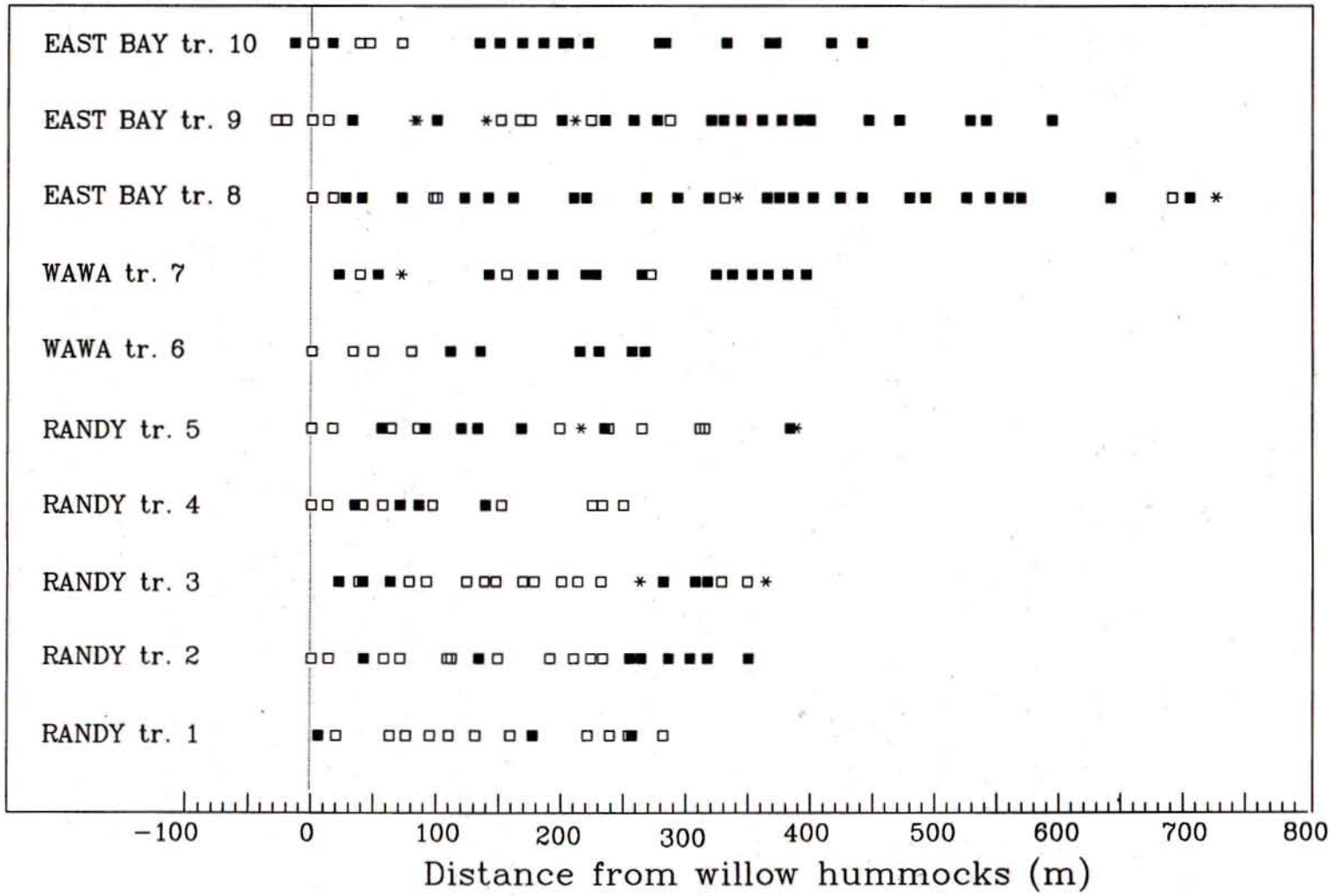
Rooted plants of both *C. subspathacea* and *P. phryganodes* can establish from single leaves and other plant fragments generated by goose grazing (Chou et al., 1992). Goose

activity may therefore enhance colonization rates of bare sediment and the mixing of different genotypes.

At La Pérouse Bay, *P. phryganodes* occurs predominately in the eastern and south-eastern salt marshes, and *C. subspathacea* in the southern salt marsh (Fig. 1.2). Specifically, *P. phryganodes* was more frequent than *C. subspathacea* in 73% of quadrats in the south-eastern and eastern salt marshes but in only 34% of quadrats in the southern salt marsh (quadrat sampling described in Chapter 3). Soil salinities are expected to be lower in the southern salt marsh than in the other salt marshes because of greater tidal and fresh water influence in the former (Chapter 3). There is also a tendency for *P. phryganodes* to occupy the less vegetated and more seaward areas of the salt marsh than *C. subspathacea* (Fig. 1.2), which may also be related to salinity differences (Chapter 4). Other researchers have also reported that *P. phryganodes* occupies more seaward areas of arctic salt marshes than *C. subspathacea* (Chapman, 1960; Kershaw, 1976; Jefferies, 1977; Jefferies et al., 1979; Glooschenko, 1980a, Glooschenko and Harper, 1982; Dignard et al, 1991) and have attributed differences in distribution to higher salinity in *P. phryganodes* dominated areas (Jefferies, 1977; MacDonald, 1977; Glooschenko, 1980a; Mason, 1981).

If *P. phryganodes* is more salt-tolerant than *C. subspathacea* (this hypothesis examined in Chapter 6), the positive feedback between graminoid growth and soil salinity should be "stronger" for *C. subspathacea*. This study concentrates on the presumed "weaker" feedback between *P. phryganodes* growth and soil salinity, since a) *Puccinellia phryganodes* is more dominant in the study area (eastern salt marsh) than *Carex subspathacea* and b) if such a positive feedback is demonstrated for *P. phryganodes* growth, then it is presumably also valid for more salt-sensitive species, including *C. subspathacea*.

Fig. 1.2. Relative frequency of *Puccinellia phryganodes* and *Carex subspathacea* in quadrats along transects (tr.) in the eastern salt marsh (East Bay), southeastern salt marsh (Wawa), and southern salt marsh (Randy) of La Pérouse Bay. In each quadrat, either *Puccinellia* was more frequent than *Carex* (■), *Carex* was more frequent than *Puccinellia* (□), or the two species were of equal frequency (*). Note that *Carex* is most frequent in the eastern salt marsh and closest to the willow hummocks. Transect numbers and salt marsh names correspond to those illustrated in Fig 3.1.


EAST BAY tr. 10
EAST BAY tr. 9
EAST BAY tr. 8
WAWA tr. 7
WAWA tr. 6
RANDY tr. 5
RANDY tr. 4
RANDY tr. 3
RANDY tr. 2
RANDY tr. 1
−100
0
100
200
300
400
500
600
700
800
Distance from willow hummocks (m)

1.6. Phenology of lesser snow geese at La Pérouse Bay

The first lesser snow geese (*Chen caerulescens caerulescens*) arrive at La Pérouse Bay between May 8-19 (data for years 1984 to 1992; Cooke and Rockwell, 1988, 1992). Nest initiation (laying of the first egg) commences 11-12 days after arrival for most pairs (Cooke et al., 1982). On average, between 3.5 and 5 eggs are laid, although this varies with year, (Cooch et al., 1989), age (Rockwell et al., 1983) and colour phase (Cooke et al., 1982). Intra-specific nest parasitism occurs frequently (Lank et al., 1989). Incubation begins a few days after the laying of the first egg, and eggs hatch after about 24 days (Cooke et al., 1982). Hatch is fairly synchronous, since late initiating birds have smaller clutch sizes (Cooke et al., 1982). Broods forage intensively on the *Puccinellia-Carex* swards of the salt marsh over the next seven weeks, which allows goslings to increase from 75-80 g at hatch (Gadallah, 1993) to an average of 850-1500 g when fully fledged (data for years 1976 to 1992; Cooch et al, 1991, 1992). By mid-August, the snow geese of La Pérouse Bay have begun their southward migration along the "central flyway", passing over southern Manitoba and western Ontario, North and South Dakota, Iowa, Arkansas and ending at the U.S. Gulf Coast (Texas, Louisiana) where the geese overwinter (Cooke et al., 1982).

The mean date of nest initiation was earlier in 1991 than in 1992 (May 24 vs. June 4, respectively; Cooke and Rockwell, 1992), as was mean date of hatch (June 19 vs. June 29, respectively; Cooke and Rockwell, 1992). The mean dates of nest initiation and of hatch were earlier in 1991 and later in 1992 than values for the previous seven years (1984 to 1990; Cooke and Rockwell, 1988, 1992). As discussed below, the spring of 1991 was both earlier and warmer than that of 1992. Time of arrival, nest initiation, and hatch dates are all advanced by an early and warm spring in Hudson Bay goose populations (Cooke et al, 1982; MacInnes et al., 1990).

1.7 Herbivory by lesser snow geese

Puccinellia-Carex swards are the preferred forage of lesser snow geese (Gadallah, 1993). In the early spring there is extensive grubbing by lesser snow geese for roots and rhizomes of these graminoids (Jefferies, 1988a,b). Above-ground growth of the vegetation has not yet commenced at this time, and nutrients and carbohydrates are still stored in below-ground matter. Initially, grubbing is restricted to sites at higher elevation and inland areas where snow has melted from the surface (Iacobelli and Jefferies, 1991), but once widespread snow melt has occurred, the edges of ponds are preferred, since geese often use pondwater to remove soil from the roots as well as for frequent bouts of drinking (B. Ganter, unpublished activity budgets). Grubbing disturbs the upper 1-2 cm of sediments as well as decreasing local plant density.

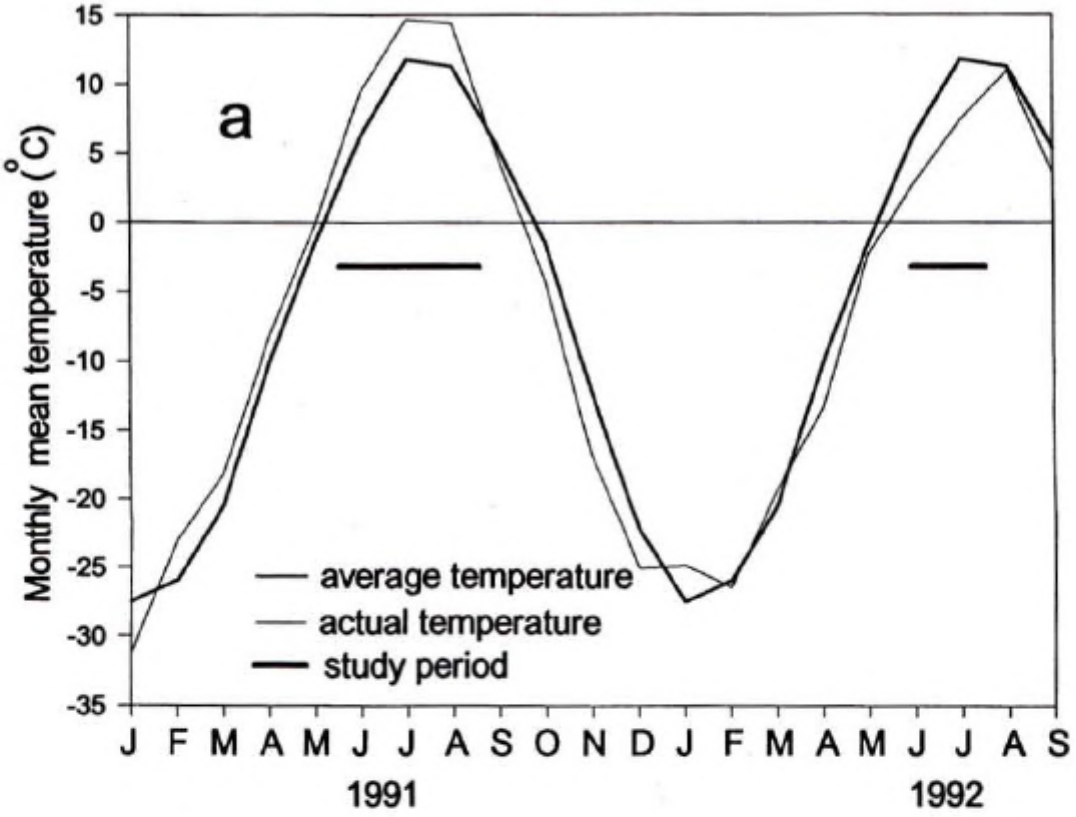
Lesser snow geese remove 60 to 90% of net above-ground primary production (NAPP) of *Puccinellia-Carex* swards (Bazely and Jefferies, 1989). Other vegetation is grazed to a much lesser extent in the summer (Jefferies, 1988b), except for inland freshwater *Carex aquatilis* and *C. X flavicans* communities (Jefferies, 1988b; Kotanen and Jefferies, 1989). Between 1979 and 1986, grazing reduced the standing crop but increased the NAPP and nitrogen content of *Puccinellia-Carex* swards at La Pérouse Bay (Cargill and Jefferies, 1984a; Bazely and Jefferies, 1989; Hik and Jefferies, 1990; Hik et al., 1991). Grazing by geese, at least in the past, has therefore resulted in a greater amount and higher nutrient content of forage. There is therefore a positive feedback cycle between goose grazing and the supply of high quality forage, caused by a grazing-dependent acceleration of the nitrogen cycle (Jefferies, 1988a). In Chapter 7, this positive feedback is described in detail and is compared to the hypothesized positive feedback cycle between soil salinity and graminoid growth.

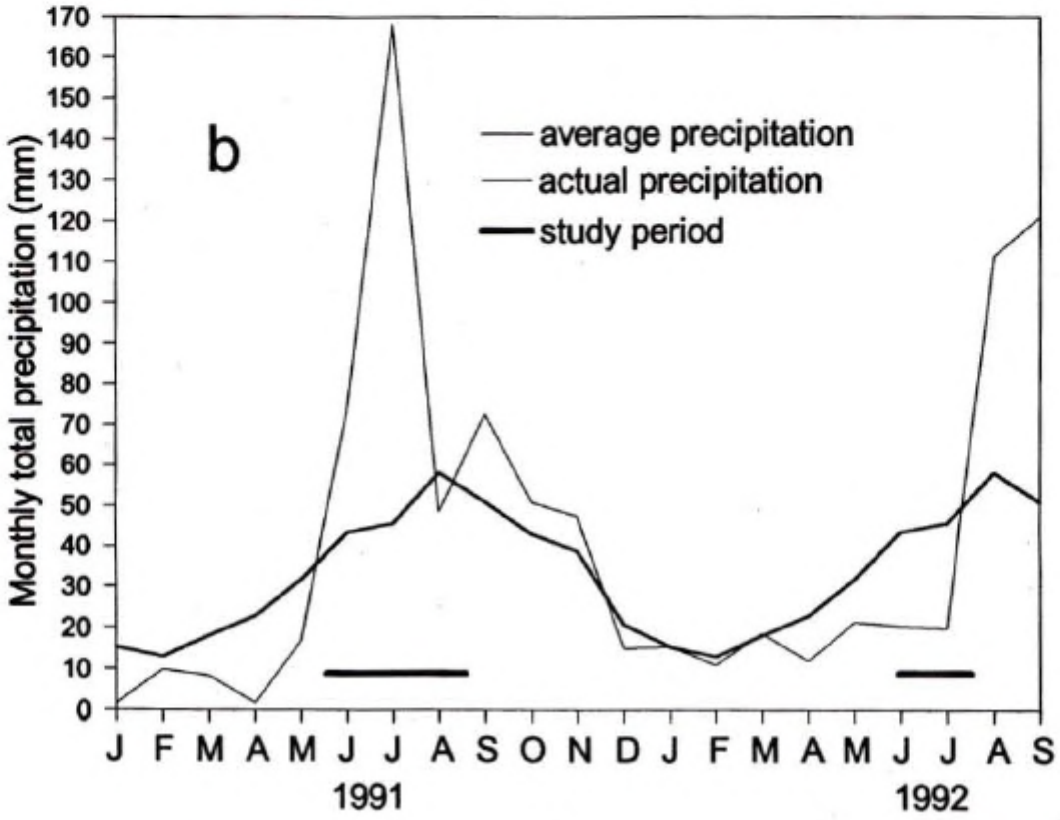
1.8 Weather

On average, daily mean temperatures are below the freezing point for seven months of the year at La Pérouse Bay (Fig. 1.3), due to the influence of the cold Arctic Air Mass (Scott, 1992). As the Arctic Air Mass contracts poleward in early spring, its southern edge or Arctic Front passes over La Pérouse Bay, and there is a sharp rise in surface temperature as a warmer air mass invades (Scott, 1992). The date the Arctic Front passes an area, therefore, denotes the beginning of climatic summer, and the rapidity with which the Arctic front passes is reported to be highly predictive of mean summer temperatures (Scott, 1992). The passing of the Arctic Front coincides with the northward migration of geese from areas near La Pérouse Bay, and rains of mature insects (Scott, 1992). On average, daily mean temperatures reach a maximum of 12°C in mid-July, and monthly total precipitation peaks in August at 58 mm (Fig 1.3).

The summers of 1991 and 1992 differed in both temperature and precipitation from average trends (based on the period 1951-1980), especially during the study periods (Fig 1.3). The summer of 1991 was both warmer and wetter than average, while the summer of 1992 was both colder and (during the study period) drier than average. On almost every day between early May and early September, air temperatures were higher in 1991 than in 1992 with the difference exceeding 5°C on half of the days, and 10°C on 24 days (Fig 1.4). This is due both to a later passing of the Arctic Front in 1992 (late May to early June) than in 1991 (mid May), and a slower increase in mean temperature after the passing of the Arctic Front in 1992 than in 1991 (Fig 1.4). The passage of the Arctic Front in 1992 may have been obscured by the influence of sea-ice as in 1986 and 1988 (Scott, 1992). Meteorologically, 1991 and 1992 were record-breaking years (data collected and compiled by Environment Canada, Churchill, Manitoba). In 1991, the temperature of six days of the month of August and two days in July exceeded previous record high temperatures (set in 1944 to 1989). In 1992, the temperature of seven days in June and six days in July was lower than previous record low temperatures (set in 1945 to 1982). The total rainfall for July was 168.2 mm in 1991, exceeding the previous record of 118.1 mm set in 1948.

Fig. 1.3. Monthly mean temperature and precipitation at Churchill, Manitoba (30 km west of La Pérouse Bay) in 1991 and 1992 compared to average values for the period 1951 to 1980. Data presented in this thesis was collected during two study periods in each of 1991 and 1992. Note that the study period of 1991 was warmer and wetter than average, and the study period of 1992 was colder and drier than average. Data supplied by Environment Canada, Churchill, Manitoba.


a
Monthly mean temperature (°C)
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
average temperature
actual temperature
study period
J F M A M J J A S O N D J F M A M J J A S
1991
1992


b
Monthly total precipitation (mm)
170
160
150
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130
120
110
100
90
80
70
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50
40
30
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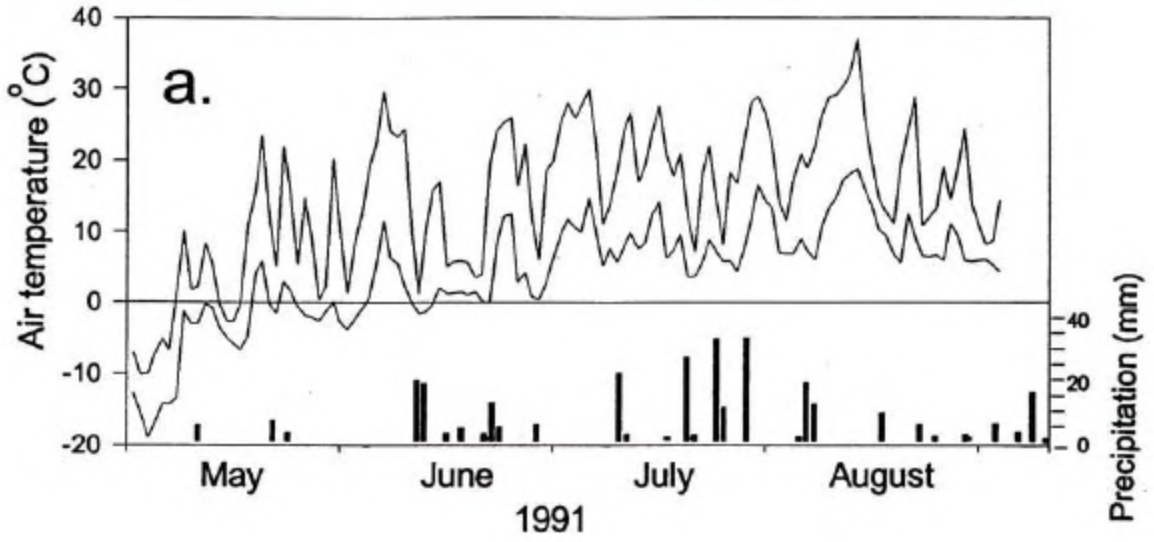
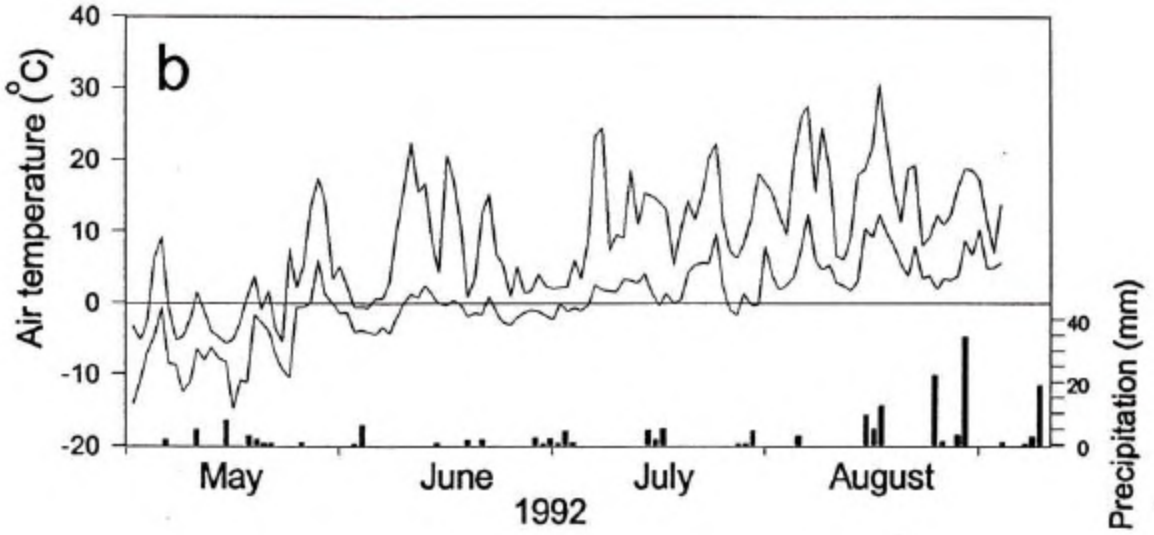
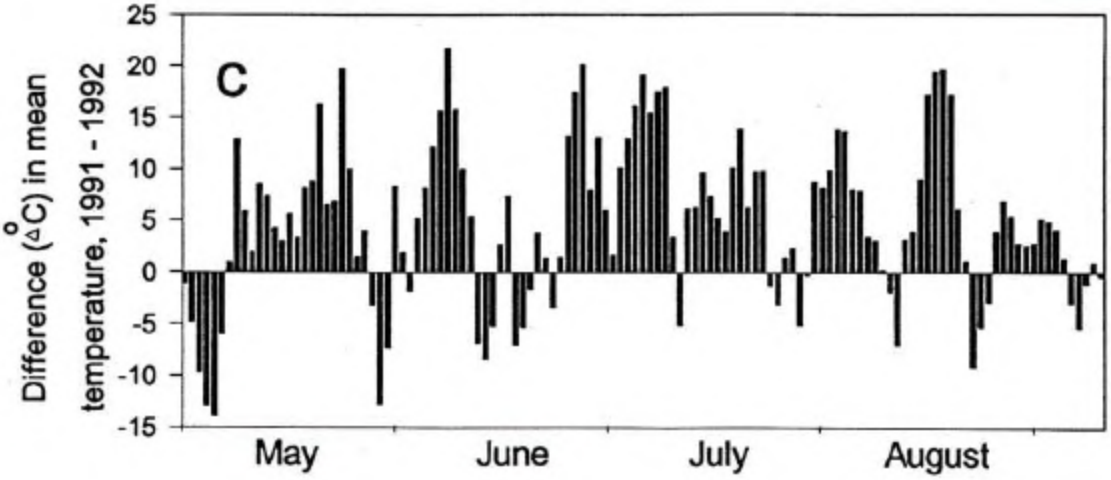
10
0
average precipitation
actual precipitation
study period
J F M A M J J A S O N D J F M A M J J A S
1991
1992

Fig. 1.4. Daily precipitation and maximum and minimum temperatures in the summer of 1991 (a) and 1992 (b) in Churchill, Manitoba (30 km west of La Pérouse Bay). Differences between 1991 and 1992 in daily mean temperatures on each date are also shown (c). Note that 1991 was warmer than 1992 on most dates between May and September, and 1991 was on average wetter than 1992 between May and August. Data supplied by Environment Canada, Churchill, Manitoba.


a.
Air temperature (°C)
40
30
20
10
0
-10
-20
Precipitation (mm)
40
20
0
May
June
July
August
1991


b
Air temperature (°C)
40
30
20
10
0
-10
-20
Precipitation (mm)
40
20
0
May
June
July
August
1992


c
Difference (°C) in mean temperature, 1991 - 1992
25
20
15
10
5
0
-5
-10
-15
May
June
July
August

CHAPTER 2: GENERAL METHODOLOGY

2.1 Categories of "high biomass", "low biomass" and "bare".

The salt-marsh vegetation at La Pérouse Bay is presently very patchy, consisting of islands of the previously extensive high biomass vegetation, surrounded by bare, grubbed regions and intermediate, partially grubbed, low biomass areas (Plates 2.1-2.4). The series "high biomass"-"low biomass"-"bare" therefore represents, on a spatial scale, stages in the degradation of the salt marsh over time. These three categories are used extensively in this study.

Above-ground biomass was measured by clipping turves (approx. 8cm x 8cm) at soil level into trays of water, separating the living (floating) from the dead (sinking) biomass, drying the live biomass for 1 week or more at 60°C and weighing the dried live biomass. Above-ground biomass was determined for the three biomass categories throughout the growing season in 1991 and 1992 (Fig. 2.1). As the 1992 growing season was approximately 2 weeks later than the 1991 growing season (Fig. 1.4, Chapter 1), 1991 mid-July values are comparable with 1992 late-July values.

High biomass areas had a mid-July above-ground biomass (mean $\pm$ SE) of 58 $\pm$ 3 g dry weight/m^2 in 1991, and a late-July biomass of 64 $\pm$ 4 g/m^2 in 1992. Low biomass areas had a mid-July above-ground biomass of 20 $\pm$ 2 g/m^2 in 1991, and a late-July biomass of 29 $\pm$ 4 g/m^2 in 1992. Bare areas had less than 1 g/m^2 biomass in both 1991 and 1992. Peak biomass in high biomass areas was therefore 2.9-fold greater than that of low biomass areas in 1991, and 2.2-fold greater in 1992.

This difference in biomass between high and low biomass areas could reflect either differences in shoot densities or in shoot mass. Shoot densities in high biomass areas were 5.7 $\pm$ 0.4 shoots/cm^2 (n=17 3cm x 3cm turves), and in low biomass areas were 0.9 $\pm$ 0.1 shoots/cm^2 (n=28 8cm x 8cm turves), giving a 6.3-fold difference in shoot densities between

Plates 2.1-2.4. The salt marsh is covered by "high biomass" vegetation (2.1), "low biomass" vegetation (2.2), and "bare" areas (2.3). Note that the exposed sediment of bare areas and of low biomass areas is covered by a dry, cracking algal crust. The flowering plant in 2.1 is *Potentilla egedii*. In more heavily grazed high biomass sites, flowering by *Potentilla egedii* is prevented by clipping of apical meristems by geese. (For scale, a 9 cm jack knife is included in 2.1-2.3). In the salt marsh, patches of high biomass vegetation are separated by bare areas, while low biomass vegetation typically is found near the edges of high biomass patches (2.4). The 1m x 1m exclosures shown in 2.4 are part of a demographic study described in Chapter 5.

2.1

2.2

2.3

2.4

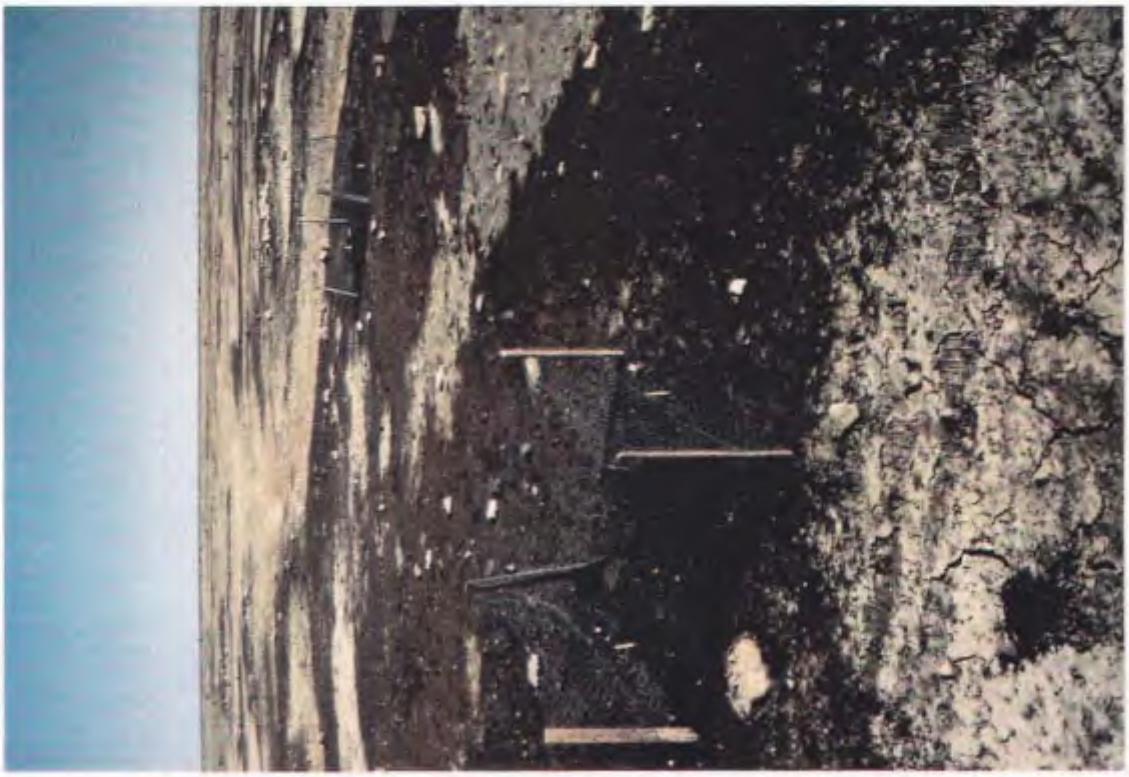
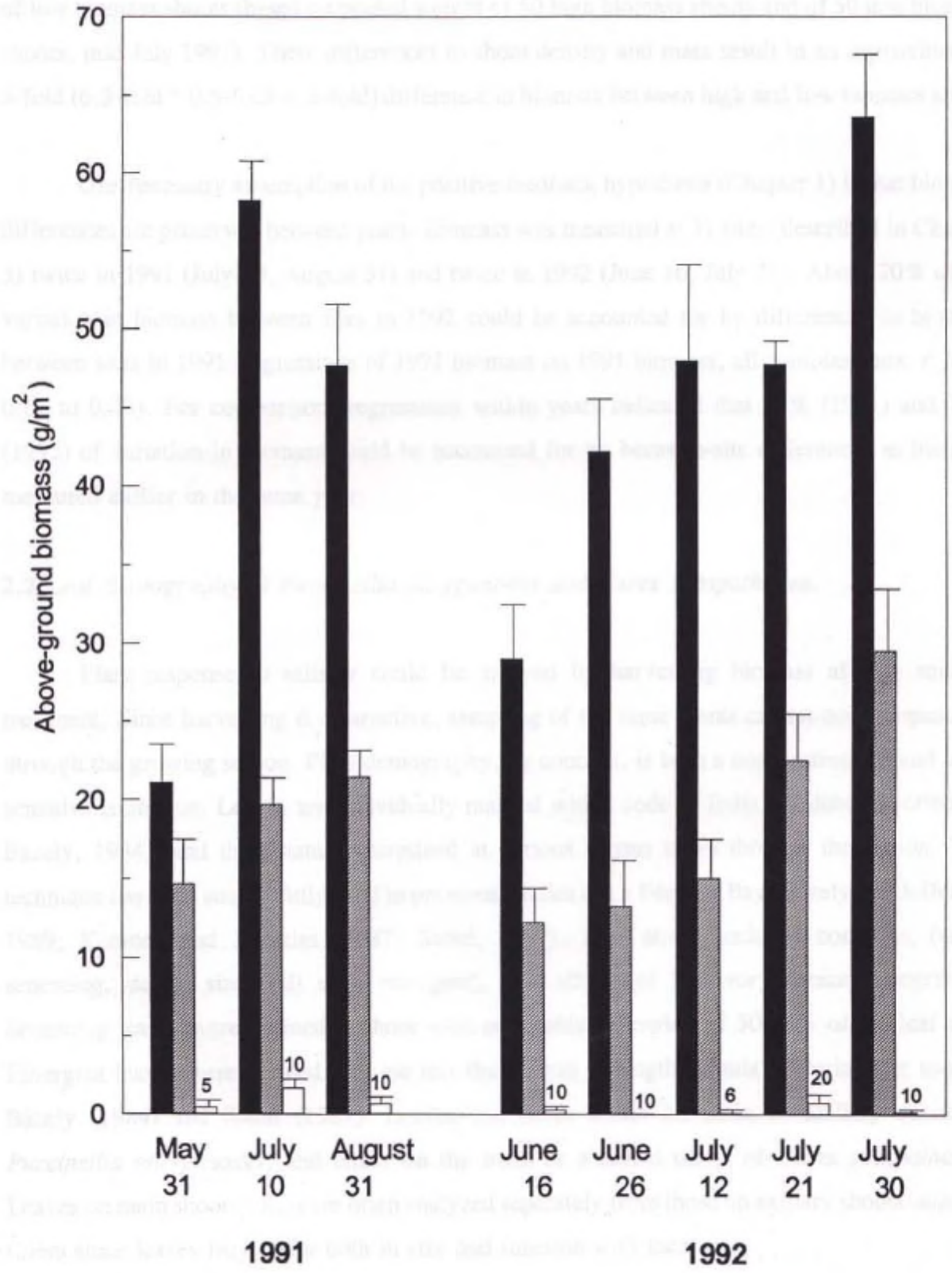


Fig. 2.1. Above-ground biomass of high biomass (solid bars), low biomass (hatched bars), and bare (open bars) sites in 1991 and 1992. Note that on almost all dates, the biomass of high biomass sites is twice that of low biomass sites. Bare sites had virtually no biomass. Sample size (sites/category) was identical for high biomass, low biomass and bare categories within each date, but not between dates, and is indicated for each date (on top of the error bar for the bare sites). Error bars are $\pm$ 1 SE.


70
60
50
40
30
20
10
0
Above-ground biomass (g/m 2)
5
10
10
10
10
6
20
10
May 31
July 10
August 31
June 16
June 26
July 12
July 21
July 30
1991
1992

high and low biomass areas. High biomass shoots had, in general, half the above-ground mass of low biomass shoots (based on pooled weight of 50 high biomass shoots and of 50 low biomass shoots, mid-July 1991). These differences in shoot density and mass result in an approximately 3-fold (6.3-fold * 0.5-fold = 3-fold) difference in biomass between high and low biomass areas.

One necessary assumption of the positive feedback hypothesis (Chapter 1) is that biomass differences are preserved between years. Biomass was measured at 31 sites (described in Chapter 3) twice in 1991 (July 10, August 31) and twice in 1992 (June 16, July 21). About 70% of the variation in biomass between sites in 1992 could be accounted for by differences in biomass between sites in 1991 (regressions of 1992 biomass on 1991 biomass, all combinations; r^2 from 0.61 to 0.73). For comparison, regressions within years indicated that 77% (1991) and 73% (1992) of variation in biomass could be accounted for by between-site differences in biomass measured earlier in the same year.

2.2 Leaf demography of *Puccinellia phryganodes* and *Carex subspathacea*.

Plant response to salinity could be assayed by harvesting biomass after a suitable treatment. Since harvesting is destructive, sampling of the same plants cannot occur repeatedly through the growing season. Plant demography, by contrast, is both a non-destructive and more sensitive technique. Leaves are individually marked with a code of India Ink dots (described in Bazely, 1984), and their status determined at various census times through the season. This technique has been successfully used in previous studies at La Pérouse Bay (Bazely and Jefferies, 1989; Kotanen and Jefferies, 1987; Sadul, 1987). Leaf status includes condition (alive, senescing, dead), size (full size, emergent), and effects of herbivory (grazed, ungrazed). Senescing leaves were defined as those with noticeable yellowing of 30-70% of the leaf area. Emergent leaves were defined as those less than 2 mm in length. Similar criteria were used by Bazely (1984) and Sadul (1987). Leaves can occur either on main or axillary shoots of *Puccinellia phryganodes*, and either on the main or attached tillers of *Carex subspathacea*. Leaves on main shoots/tillers are often analyzed separately from those on axillary shoots/attached tillers since leaves may differ both in size and function with location.

There are two possible methods by which demographic data can be analyzed, referred to as "seasonal" and "interval-based" throughout this thesis.

Leaf birth rate is calculated by the seasonal method as the total number of new leaves observed over the study period divided by the number of days of the study period. Similarly, leaf death rate is calculated by the seasonal method as the number of leaves that died over the study period divided by the number of days of the study period.

Leaf birth rates are calculated by the interval-based method as the inverse of the mean interval (in days) between successive leaf births. Similarly, leaf death rates are calculated by the interval-based method as the inverse of the mean interval (in days) between successive leaf deaths. For the interval-based method, therefore, it is necessary to estimate the birth date and death dates of leaves. Leaves first observed as fully expanded leaves at $census_t$ are assumed to be born at the mid-point of the interval between $census_{t-1}$ and $census_t$. Leaves first observed as emergent at $census_t$ are assumed to be born at the three-quarters point of the interval between $census_{t-1}$ and $census_t$. Leaf death date is calculated similarly. Leaves observed as living at $census_{t-1}$ and dead at $census_t$ are assumed to have died at the mid-point of the interval between $census_{t-1}$ and $census_t$. Leaves observed as senescent at $census_{t-1}$ and dead at $census_t$ are assumed to be born at the three-quarters point of the interval between $census_{t-1}$ and $census_t$. Obviously, the underlying assumption is that, in terms of time, emergent leaves are half-grown and senescent leaves are half-dead!

Seasonal demographic parameters are not affected by the number or length of intervals between censuses, since births and deaths are summed over the entire season. Interval-based demographic parameters will be more accurate with many closely spaced censuses than just a few. The two methods will tend to calculate similar values of leaf birth or death rates when leaf births or deaths are regularly spaced over the study period. If leaf births or deaths are clustered in time, however, the interval-based method will tend to produce higher values of leaf birth or death rates than the seasonal method. In this case, values from both methods are valid but estimate different quantities. The seasonal method estimates leaf births and deaths over the entire

study period, while the interval-based method estimates leaf and death rates over the fastest-growing or -dying period. There is a limit on speed of leaf birth and death rates, however, in the interval-based method: if the mean interval between leaf births or deaths is zero no meaningful birth or death rate can be calculated (the inverse of zero is infinity). By contrast, a value can be calculated by the seasonal method in this case. Further complexities arise with axillary shoot leaves. Some plants produce none or only one axillary shoot leaf. In this case, a value will be assigned by the seasonal method, but no value can be calculated by the interval-based method. The interval-based method, therefore, calculates birth rate not only over the fastest growing period but also for the fastest growing plants. Selection of a method, therefore, depends on whether average or optimal plant performance is of interest. In most cases in this study, it is desirable to extrapolate results from individual plant performance to vegetation performance per unit area, so seasonal demographic parameters are of most interest. For a study of leaf demography of transplanted plants (Chapter 5), results using interval-based leaf birth and death rates are provided in an appendix for comparison.

Leaf lifespan can only be calculated by an interval-based method. The lifespan of an individual leaf is the difference (in days) between its birth and death. Birth and death dates are calculated as described earlier. Values of lifespan are averaged for all leaves of a given plant for which this information is available. Again, this formula weights the mean value to periods of high turnover and for plants with high turnover rates. At least three census dates are necessary to record the birth and death of a leaf and hence generate a value for leaf lifespan. With three census dates, however, these values of birth date, death date, and hence lifespan will be identical for all leaves (save some variability introduced by emergent leaves) so a minimum of four census dates is needed to obtain differences between plants. Leaf lifespan is therefore only calculated for the demography analysis of transplanted plants in 1991 (Chapter 5; five census dates) and is presented in an appendix. Although leaf lifespan cannot be directly calculated by the seasonal method, leaf turnover rate (the inverse of leaf lifespan) will be highest when both leaf birth and death rates are high and lowest when both leaf birth and death rates are low.

The following abbreviations are used for seasonal demographic parameters for *Puccinellia phryganodes* :

MSLB (main shoot leaf birth rate)
MSLD (main shoot leaf death rate)
ASLB (axillary shoot leaf birth rate)
ASLD (axillary shoot leaf death rate)
TLB (total leaf birth rate)
TLD (total leaf death rate)

"Total" refers to main and axillary shoot leaves summed for each plant. The following abbreviations are used for interval-based demographic parameters for *Puccinellia phryganodes*:

MSBR (main shoot leaf birth rate)
MSDR (main shoot leaf death rate)
ASBR (axillary shoot leaf birth rate)
ASDR (axillary shoot leaf death rate)
MSLL (main shoot leaf lifespan)
ASLL (axillary shoot leaf lifespan)

For *Carex subspathacea* leaf demography, main tiller replaces main shoot (MT replaces MS) and attached tiller replaces axillary shoot (AT replaces AS) in the above explanation. Leaf births, deaths, and lifespans are pooled for all axillary shoots or attached tillers for each plant since only differences from main shoot/tiller demography are of interest (ie., differences among axillary shoots/attached tillers are not of interest).

Demographic data is calculated for all plants, when possible, including plants which die during the course of the experiment. Plant death occurs when leaf death rates exceed leaf birth rates and is therefore part of a continuum of leaf demographic patterns. Plant mortality data is presented separately as well.

Interval-based and seasonal demographic data for transplanted plants (Chapter 5) was calculated using a BASIC computer program (Demography, version 2.0) developed by Dawn Bazely (York University, Canada) and Alistair Inman (University of Toronto, Canada).

2.3 Soil water extraction by centrifugation and subsequent sodium analysis

Blocks of soil, approximately 10 cm x 10 cm x 2 cm deep, were collected. The top centimeter of soil was removed and pressed into 5 cc syringe casings. These were centrifuged 5 min at high speed, and the soil water collected in 20 ml centrifuge tubes in which the syringe casings sat. The extracted soil water was diluted with deionized water, frozen, and later analyzed for sodium by flame spectrophotometry (facilities provided by V. Timmer, Forestry Dept., University of Toronto). Centrifugation has previously been used as a method to extract soil water for salinity determination (eg., Price and Woo, 1988a).

CHAPTER 3: PLANT COMMUNITIES OF LA PÉROUSE BAY SALT MARSHES

3.1. Introduction

Large-scale destruction of salt-marsh vegetation has been reported at La Pérouse Bay, Manitoba (Chapter 1; Williams et al., 1993). Specifically, previously intact swards of *Puccinellia phryganodes* and *Carex subspathacea* have been recently converted to bare mud flats in many areas. The future vegetation structure of the salt marsh will depend, in part, on which plant communities will replace these bare mud flats, and how long this process will take. To provide a framework for analyzing revegetation potential and direction, a large-scale survey of the plant communities and bare degraded areas of the La Pérouse Bay salt marshes was undertaken. The objectives of this study were to a) to quantify the extent and distribution of bare degraded areas, b) to describe the plant communities of the salt marshes, and c) interpret differences between plant community types and bare degraded areas on the basis of environmental variables. Canonical correspondence analysis is used to both describe communities and relate them to environmental variables. Although bare degraded areas are without plants, recording of selected physical features as well as plant species allowed them to be included in the canonical correspondence analysis. The vegetation of several Hudson and James Bay coastal marshes has been described earlier (Ritchie, 1956; Kershaw, 1976; Glooschenko and Martini, 1978; Jefferies et al., 1979; Glooschenko, 1978, 1980 a,b; Ringius, 1980; Glooschenko and Harper, 1982; Ewing and Kershaw, 1986; Dignard et al., 1991), but these description have been largely restricted to field observations and direct gradient analysis along transects. Ordination or clustering techniques have been previously used in only one such study (Ewing and Kershaw, 1986).

3.2. Methods

Extensive salt marshes surround the eastern and southern portions of La Pérouse Bay (islands and smaller areas of salt marsh characterize the western shore). The landward extent of the salt marsh is demarcated by the "willow edge", an abrupt interface between the inland

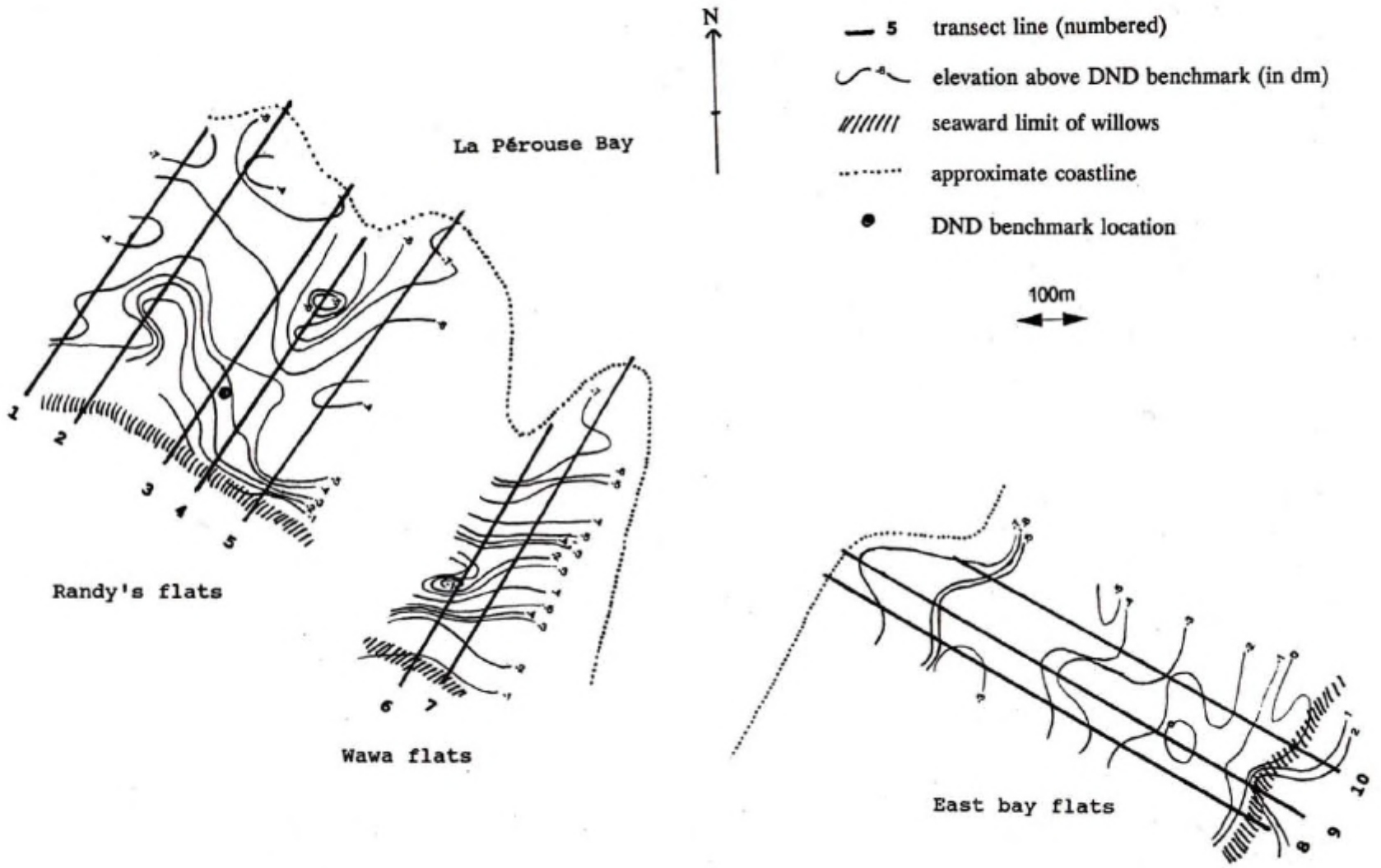
Salix bushes/*Festuca-Calamagrostis* communities and the salt marsh, which is fairly linear over several hundred meters.

A total of ten transects were established on the southern and eastern marshes of La Pérouse Bay in 1991 (Fig 3.1). Five of these transects were located on the southern salt marsh between two streams ("Randy's flats"). Two transects were located on the southeastern salt marsh just west of the main creek of the Wawa River ("Wawa flats"). Three transects were located on the more vegetated and southern portion of the eastern salt marsh ("East Bay flats"). The willow edge within each flat was divided into a suitable number of adjacent 100 m segments, and a transect was randomly located in each segment. Within each of the flats, transect lines were parallel to each other and orientated perpendicular to the direction of the willow edge.

Each transect began in *Festuca-Calamagrostis* communities about 20 m inland from the willow edge, proceeded across the salt marsh, and ended at the low tide shoreline. The length of transects varied from 282 to 412 m on Randy's flats, from 267 to 384 m on Wawa flats, and from 456 to 727 m on East Bay flats, for a total of 4.27 km of transects. Each transect was divided into 15 m segments, and a 25 x 25 cm quadrat was randomly located in each segment for a total of 290 quadrats. The quadrat size and interval between quadrats were selected to allow a representative survey of large area of marsh. Similar surveys of Hudson and James Bay salt marshes have used 50 to 100 cm square quadrats placed at intervals of 10, 20 or 30 m apart (Kershaw, 1976; Glooschenko and Martini, 1978; Glooschenko, 1980a; Ringius, 1980; Ewing and Kershaw, 1986).

The quadrat was composed of 25 adjacent cells of 5 cm x 5 cm. Between July 28 and August 11, 1991, species presence/absence was recorded for each cell (nomenclature follows Porsild and Cody, 1980). Moss was not identified to species in the field. Earlier studies in this area found *Bryum inclinatum* and *Campylium stellatum* to be common species of moss (Jefferies et al., 1979a). Selected physical phenomena were also recorded in each cell, including exposed grey mineral soil (covering > 50% of the cell), stones (from gravel to

Fig. 3.1. Topography of the salt-marsh flats (Randy's, Wawa and East bay flats) surrounding La Pérouse Bay. Contour lines indicate points of similar elevation, relative to a DND benchmark. Since this benchmark was more elevated than much of the salt marsh, the elevation of most contour lines is negative. Elevations were determined every 20 to 50 m along transects, so small pools are not visible at this resolution and contour lines are most accurate near transect lines. Transect lines were laid down as described in the text.


N
5 transect line (numbered)
elevation above DND benchmark (in dm)
seaward limit of willows
approximate coastline
DND benchmark location
100m
La Pérouse Bay
Randy's flats
Wawa flats
East bay flats

boulders), ice rafts (thick turves of soil and/or vegetation deposited on the marsh by spring ice action), large cracks, light brown algal blisters and black algal blisters. Algal blisters are formed by the drying, wrinkling, and cracking of a thick algal crust that covers much of the unvegetated salt-marsh (Golubić, 1973). Differences in colour of algal blisters may represent different species composition. Frequency was calculated as the proportion of cells in a quadrat in which a given species or physical phenomenon was present. Kershaw (1976) suggested that frequency is the best measure of species abundance in the upper salt marsh. Lastly, the presence of only dead graminoids (usually accompanied by exposed roots) in a quadrat was noted, and given an arbitrary frequency of 1/25. It may seem unusual for the frequency of physical phenomena to be recorded along with species frequency, but it is appropriate in this system where a large proportion of the area is unvegetated or poorly vegetated.

Various environmental measurements were recorded at the site of each quadrat, including vegetation cover (%) in the entire quadrat, depth of standing water (semi-dry pond bottoms were assigned an arbitrary value of 0.1 cm water), depth of the dark brown organic layer in the soil, and depth of the black reduced layer of the soil. Not all sites had soil with an organic layer or a reduced layer, and most sites were dry (water depth = 0 cm). Elevation of each quadrat (relative to a Department of National Defense benchmark) was determined by quick-set level and surveying staff. The Department of National Defense declined to provide information on the height of this benchmark, so this benchmark was set at an arbitrary zero. The distance of each quadrat from the willow edge was recorded.

Canonical correspondence analysis (CCA) was used to identify species/ physical phenomena associations using the frequency data, and to relate between-site differences in these associations to environmental variables. Standard and detrended correspondence analysis (CA and DCA respectively) and CCA can all be used to relate species associations to environmental variables, by using a combination of ordination and regression (Ter Braak, 1988). In CA and DCA, after the final iteration of the weighted-averaging algorithm, an ordination diagram of species and sites is generated, and the researcher may then regress

environmental variables against the ordination axes. The orientation of an ordination axis, however, may not be the direction best correlated with a given environmental variable. This problem is corrected by CCA, which regresses samples scores on environmental variables after each iteration, so that the resultant orientation of the ordination axes reflects statistically-important environmental gradients. Which environmental variables are most important can be deduced by their correlation with the species axes consisting of sample scores (inter-set correlations).

Inter-set correlations are reported here rather than canonical coefficients since the latter may be destabilized by strong correlations between environmental variables (Ter Braak, 1988).

The program CANOCO was used for all CCA analyses (Ter Braak, 1988).

3.3 Results

A total of 29 plant species were encountered in the survey, in addition to 7 types of physical phenomena (Table 3.1).

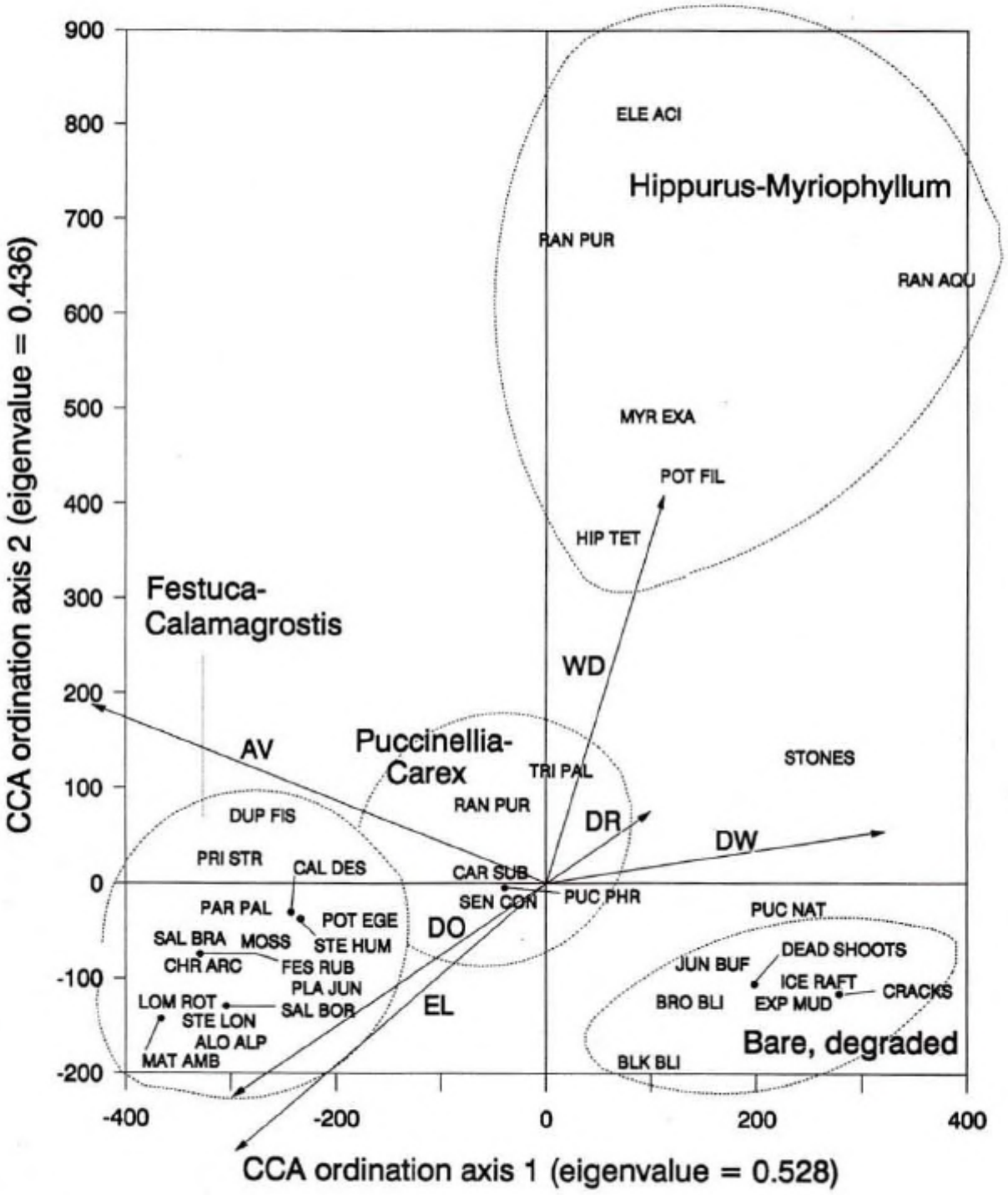
Associations between plant species/physical phenomena were explored using CCA. In a CCA of all sites, the species/phenomena were separated into four groups (Fig. 3.2). The first ordination axis (eigenvalue = 0.528) separated a *Festuca-Calamagrostis* community from bare degraded areas, with a *Puccinellia-Carex* salt-marsh community occupying an intermediate position between these extremes. The second and only slightly weaker ordination axis (eigenvalue = 0.436) separated a *Hippurus-Myriophyllum* community from the *Puccinellia-Carex* community and bare degraded areas. Together, the two axes accounted for 80.3% of the total variance. The third and fourth axes were relatively unimportant (eigenvalues = 0.142 and 0.063 respectively).

The *Festuca-Calamagrostis* community is characterized by species such as the shrub

Table 3.1. Plant species and physical phenomena encountered in the survey and their abbreviations (used in Fig. 3.2.).

Physical phenomena	
Black algal blisters	BLK BLI
Light brown algal blisters	BRO BLI
Large cracks	CRACKS
Exposed mineral soil (>50% cell area)	EXP MUD
Ice rafted substrate	ICERAFT
Pebbles and boulders	STONES
Plant species	
Alopecurus alpinus	ALO ALP
Calamagrostis deschampsioides	CAL DES
Carex subspathacea	CAR SUB
Chrysanthemum arcticum	CHR ARC
Dupontia fisheri	DUP FIS
Eleocharis acicularis	ELE ACI
Festuca rubra	FES RUB
Hippurus tetraphylla	HIP TET
Juncus bufonius	JUN BUF
Lomatagonium rotatum	LOM ROT
Matricaria ambigua	MAT AMB
Moss	MOSS
Myriophyllum exalbescens	MYR EXA
Parnassia palustris	PAR PAL
Plantago juncoides	PLA JUN
Potamogeton filiformis	POT FIL
Potentilla egedii	POT EGE
Primula stricta	PRI STR
Puccinellia nuttalliana	PUC NAT
Puccinellia phryganodes	PUC PHR
Ranunculus aquatilis	RAN AQU
Ranunculus cymbalaria	RAN CYM
Ranunculus purshii	RAN PUR
Rumex occidentalis	RUM OCC
Salicornia borealis	SAL BOR
Salix brachyocarpa	SAL BRA
Senecio congestus	SEN CON
Stellaria humifusa	STE HUM
Stellaria longipes	STE LON
Triglochin palustris	TRI PAL

Fig. 3.2. Biaxial plot (first two CCA axes) of the ordination of plant species and physical phenomena (abbreviations given in Table 3.1). Species and physical phenomena tend to separate into four distinct communities, named and exclosed in subjectively positioned dashed lines. Arrows represent the magnitude and direction of correlations of six environmental variables with each of the two CCA axes; WD=water depth, EL=elevation, DR=depth of the reduced layer, DW=distance from willows, DO=depth of the organic soil, AV=percent of area covered with vegetation.


CCA ordination axis 2 (eigenvalue = 0.436)
CCA ordination axis 1 (eigenvalue = 0.528)
900
800
700
600
500
400
300
200
100
0
-100
-200
-400
-200
0
200
400
ELE ACI
Hippurus-Myriophyllum
RAN PUR
RAN AQU
MYR EXA
POT FIL
HIP TET
Festuca-
Calamagrostis
WD
AV
Puccinellia-
Carex
TRI PAL
STONES
RAN PUR
DR
DW
DUP FIS
PRI STR
CAL DES
CAR SUB
SEN CON
PUC PHR
PAR PAL
POT EGE
DO
PUC NAT
SAL BRA
MOSS
STE HUM
DEAD SHOOTS
CHR ARC
FES RUB
JUN BUF
ICE RAFT
PLA JUN
CRACKS
LOM ROT
SAL BOR
EL
BRO BLI
EXP MUD
STE LON
ALO ALP
Bare, degraded
MAT AMB
BLK BLI

Salix brachycarpa, the graminoids *Festuca rubra* and *Calamagrostis deschampsioides*, and by a group of small dicotyledons such as *Primula stricta, Stellaria longipes, Parnassia palustris* and *Chrysanthemum arcticum* (Fig 3.2).

The *Puccinellia-Carex* community is characterized (Fig. 3.2) by the graminoids *Puccinellia phryganodes* and *Carex subspathacea*, and occasionally *Triglochin palustris*. Frequently associated dicotyledons are *Ranunculus cymbalaria, Potentilla egedii*, and *Plantago juncoides*. The latter two dicotyledons are also frequently found in the *Salix-Festuca-Calamagrostis* community, so are in an intermediate position between the two communities on the ordination diagram. *Senecio congestus* is found mainly in areas of disturbance and wrack cover in the *Puccinellia-Carex* salt marsh.

The bare degraded areas are entirely or almost unvegetated, with light brown and black algal blisters, exposed grey mineral sediment, and deeply cracking soil. Notably, dead graminoid shoots and exposed roots are associated with these soil conditions (Fig. 3.2). Blistering and cracking indicate the dryness of the soil, and the presence of exposed mineral soil and roots is indicative of eroding upper soil layers.

The *Hippurus-Myriophyllum* community (Fig. 3.2) is aquatic. *Hippurus tetraphylla* is found in slow-moving streams, ponds, flooded areas, semi-dry pond bottoms, and occasionally even in dry *Puccinellia-Carex* swards. *Myriophyllum exalbescens* is found in faster moving water. Also associated with this community are *Potamogeton filiformis, Ranunculus aquatilis, R. purshii*, and *Eleocharis acicularis*.

Differences between these four communities can be related to environmental variables. The six environmental variables measured were percent of quadrat area covered with vegetation, depth of the organic layer, depth of the reduced layer, depth of standing water, elevation, and distance from the willow edge. The first ordination axis was highly correlated with area covered by vegetation ($r=-0.77$, inter-set correlation), and less so with distance ($r=0.56$), organic depth ($r=-0.54$), and elevation ($r=-0.53$). The second ordination

axis was highly correlated with water depth (r=0.70), and less so with elevation (r=-0.49), organic depth (r=-0.38), and area covered by vegetation (r=0.31). The depth of the reduced layer was poorly correlated with both axes ($r < 0.14$). The direction and magnitude of the covariance between weighted averages of species and specific environmental variables can be seen in a species-environment biplot (Fig 3.2).

Average ($\pm$ SD) values of environmental variables were calculated for the 40 sites with ordination scores closest to that of each of the bare degraded community, the *Puccinellia-Carex* community, and the *Hippurus-Myriophyllum* community, and for the 12 sites representing the *Festuca-Calamagrostis* community.

The *Hippurus-Myriophyllum* sites were all in ponds or streams or had standing water (mean depth 11 cm $\pm$ 1), while only 4% of the other sites had any standing water, and that water was a maximum of 2 cm deep. This is consistent with strong correlation of water depth with the second CCA axis.

The percentage of area covered by vegetation was lowest in the bare degraded areas (0.18% $\pm$ 0.07), with a range of values only from 0 to 2%. Sites representing the *Puccinellia-Carex* community had a mean of 45.4% ($\pm$ 5.3) of area covered by vegetation, but these sites had a wide range of area covered by vegetation (from 1 to 90%). The highest percentage of area covered by vegetation was in the *Festuca-Calamagrostis* community, with a mean of 95.8% ($\pm$ 1.6) and a range from 80 to 100%. Additional CCAs with aquatic *Hippurus-Myriophyllum* sites absent, and then with both *Hippurus-Myriophyllum* and *Festuca-Calamagrostis* sites absent indicate that the percent of area covered by vegetation is the main difference between non-aquatic salt-marsh communities (Table 3.2).

The *Festuca-Calamagrostis* sites were, on average, 40 cm higher in elevation than the *Puccinellia-Carex* or bare degraded sites, but there was no difference in elevation between the latter two communities (relative elevation: 0 cm $\pm$ 5, -40 cm $\pm$ 3 cm, -41 cm $\pm$ 2 cm respectively).

Table 3.2. Inter-set correlations between environmental variables and the first two CCA axes. Environmental variables include the percentage of area covered by vegetation (% vegetated), water depth, elevation, distance from the willow line (distance), depth of organic soil (organic soil), and depth of reduced soil (reduced soil). Unless otherwise noted, the data set includes all sites. Inter-set correlation coefficients are not presented for some variables because they are either covariables in the analysis, or because the variability of these variables was negligible after certain sites were excluded from the analysis.

DATA SET:	ALL SITES		NO AQUATIC SITES		NO AQUATIC OR FESTUCA SITES	
variate	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
% vegetated	-0.774	+0.313	-0.826	+0.247	+0.782	+0.090
water depth	+0.161	+0.696	----	----	----	----
elevation	-0.527	-0.491	-0.522	-0.572	-0.080	-0.553
distance	+0.563	+0.083	+0.586	+0.326	-0.236	+0.520
organic soil	-0.541	-0.376	-0.525	-0.412	+0.140	-0.526
reduced soil	+0.138	+0.116	+0.155	+0.274	+0.050	+0.212
eigenvalue	0.528	0.436	0.545	0.230	0.380	0.170

COVARIABLE:	% VEGETATED		DISTANCE		ORGANIC SOIL	
variate	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
% vegetated	----	----	+0.520	-0.644	+0.769	-0.313
water depth	+0.701	+0.366	+0.621	+0.465	+0.409	+0.664
elevation	-0.691	+0.345	-0.473	-0.387	-0.094	-0.326
distance	+0.334	-0.363	----	----	-0.322	+0.097
organic soil	-0.594	+0.315	-0.308	-0.385	----	----
reduced soil	+0.165	-0.192	+0.094	+0.012	+0.024	-0.081
eigenvalue	0.450	0.161	0.439	0.331	0.471	0.256

COVARIABLE:	ELEVATION		WATER DEPTH		WATER DEPTH AND % VEGETATED	
variate	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
% vegetated	+0.798	-0.220	-0.811	+0.227	----	----
water depth	+0.340	+0.685	----	----	----	----
elevation	----	----	-0.449	-0.606	-0.732	+0.082
distance	-0.403	-0.011	+0.542	+0.326	+0.533	+0.204
organic soil	+0.164	-0.159	-0.477	-0.475	-0.632	-0.091
reduced soil	-0.005	-0.070	+0.119	+0.269	+0.277	+0.057
eigenvalue	0.483	0.237	0.524	0.230	0.260	0.068

The *Festuca-Calamagrostis* sites also had a mean of 73 mm (± 4) of organic soil, greater than the *Puccinellia-Carex* sites (26 mm ± 4) or the bare degraded sites (10 mm ± 3). All of the *Festuca-Calamagrostis* sites had at least 50 mm of organic layer, while 25% of the *Puccinellia-Carex* sites and 75% of the bare degraded sites had no organic layer.

In terms of position, all of the *Festuca-Calamagrostis* sites were far inland, usually not more than 20 m seaward of the willow edge, while the *Puccinellia-Carex* and bare degraded sites were scattered over the salt marsh. *Puccinellia-Carex* sites were, on average, slightly more inland (distance from willow edge 223 m ± 18) than bare degraded sites (330 m ± 29).

Communities were not equally distributed among the three salt-marsh flats. Aquatic sites accounted for 35% of sites on Randy's flats and 43% of sites on Wawa flats, but less than 12% of sites on East Bay flats. Aquatic sites on Randy's and Wawa flats include freshwater streams and ponds with 5 to 10 cm water, but on East Bay the only aquatic sites were semi-dry pond bottoms and shoreline puddles.

Of the non-aquatic sites surveyed, Randy's flats had the most vegetation cover. Sites with more than 80% cover accounted for 33% of non-aquatic sites on Randy's flats but only 15% and 13% of non-aquatic sites on Wawa and East Bay flats respectively. Similarly, 74% of non-aquatic sites on both Wawa and East Bay flats had less than 20% cover, but only 40% of those on Randy's flats had less than 20% cover. Most sites with under 20% cover were completely bare in all flats. (Sites inland of willow edge were excluded in the above analyses).

Several of the environmental variables are highly intercorrelated. For example, the three strongest correlations are between elevation and organic depth ($r=0.74$), elevation and distance ($r=-0.60$), and organic depth and distance ($r=-0.54$). It is possible that strong correlations of certain environmental variables with the ordination axes (in the original CCA of all sites) could be caused, in part, by such correlations between environmental variables.

Partial-CCAs allow the effect of covariance with other important variables to be removed from the correlation of an environmental variable with the ordination axes. Partial-CCAs of the full data set were run with each of area covered by vegetation, water depth, distance, organic depth, and elevation as covariate (Table 3.2). Depth of the reduced layer was shown earlier to be unimportant.

Since the two ordination axes are of similar strength, some of the partial CCAs resulted in exchange of the two ordination axes (ie., rotation of the ordination diagram by 90°) or rotation by 45°. Therefore, results of the partial CCAs can be interpreted in terms of the entire biaxial ordination diagram, but not in terms of specific axes.

The important environmental variables, in order of decreasing correlation with one (either) of the first two axes of the original CCA, were area covered by vegetation, water depth, distance, organic depth, and elevation (Table 3.2). In all partial CCAs, area covered by vegetation and water depth remained the variables with the strongest correlation with either axis (Table 3.2). Their importance appears to be robust.

In partial CCAs with each of area covered by vegetation, water depth, distance and organic depth as covariates, the variable with the strongest correlation with either axis, after that of area covered by vegetation and water depth, was elevation (Table 3.2). This indicates that the importance of elevation is not dependent on covariance with one other environmental variable. It could be argued that its importance is due to correlations with two variables, specifically water depth ($r=-0.31$) and area covered by vegetation ($r=0.23$), since at least one of these two variables is present in each of the previously mentioned partial CCAs. A partial CCA with both water depth and area covered by vegetation as covariates, however, indicates that of the remaining variables elevation has the strongest correlation with either axis ($r=-0.73$ with the first axis; Table 3.2). This corroborates the importance of elevation.

Therefore, area covered by vegetation, water depth, and elevation are the three most important variables in the original CCA. Distance and organic depth appear to be slightly

less important than elevation, despite having stronger correlations with the first axis of the original CCA. There are several explanations for this result. The original importance of distance may be due, in part, to its correlation with vegetated area (r=-0.38). Indeed, in a partial CCA with vegetated area as covariate, distance was more weakly correlated with either axis than was elevation or organic depth (Table 3.2). The original importance of organic depth could have been due to correlation with distance (r=-0.54) or vegetated area (r=0.28); in partial CCAs with either distance or vegetated area as covariate organic depth is not as strongly correlated as elevation with either axis (Table 3.2). Lastly, since the orientation of the original CCA axis was largely determined by vegetated area and water depth, this orientation might not have given the highest correlation of the axes with elevation. Elevation is actually almost equally well correlated with both axes of the original CCA (r=-0.53 and -0.49 for first and second axes respectively), unlike distance and organic depth. In the partial CCA with both water depth and vegetated area as covariates, elevation is strongly correlated with only one axis, and has a stronger correlation than organic depth or distance with this axis (Table 3.2).

3.4 Discussion

The salt marsh around La Pérouse Bay can be divided into four communities. The *Festuca-Calamagrostis* community occurs at the inland extreme of the salt marsh, where the organic layer is thick and well developed and the ground elevated above the salt marsh in hummocks. The rest of the salt marsh is either partially vegetated in *Puccinellia-Carex* swards or completely unvegetated in bare degraded areas. The latter bear evidence of drying and erosion, have no organic layer, and are associated with dead graminoids. A *Hippurus-Myriophyllum* community characterizes the aquatic habitat in the salt marsh.

These communities are similar to those of the "arctic zone" salt marshes of the north-east coast of James Bay described by Dignard et al. (1991). These salt marshes also had large areas with no vegetation, a *Puccinellia phryganodes* dominated community, a more inland *Carex subspathacea-Carex salina* dominated community, and a *Festuca-Calamagrostis*

community. (Together, the species composition of the *Puccinellia phryganodes* and *Carex subspathacea-Carex salina* communities is similar to that of the *Puccinellia-Carex* community of this study). The *Puccinellia-Carex* community of this study is consistent with the dominance of *Puccinellia phryganodes* and, to a lesser extent, *Carex subspathacea* in other salt marshes on the arctic coast of North America (Porsild, 1957; Jefferies, 1979; Vince and Snow, 1984) and James and Hudson Bays (Kershaw, 1976; Glooschenko and Martini, 1978; Glooschenko, 1978, 1980 a,b; Ringius, 1980; Glooschenko and Harper, 1982; Ewing and Kershaw, 1985).

In this study, communities were separated on the first CCA axis on the basis of area covered by vegetation, depth of the organic layer, elevation, and distance inland and on the second CCA axis on the basis of standing water (Table 3.2). These results are similar to those obtained from a detrended correspondence analysis (DCA) of the vegetation of a James Bay salt marsh by Ewing and Kershaw (1985). In their analysis, the first DCA axis separated communities on the basis of vegetation species richness, depth of the organic layer, elevation, and distance inland, while the second DCA axis separated communities on the basis of standing or tidal water and soil salinity. Although vegetation richness was not specifically measured in the study at La Pérouse Bay, it is expected to be also strongly correlated with the first CCA axis.

In this study, multivariate analysis indicated that the non-aquatic communities occupy a complex gradient of vegetation cover, elevation, organic soil development, and seaward distance, as summarized by the first CCA axis (Fig 3.2). This can be thought of as a successional gradient, where a densely vegetated *Festuca-Calamagrostis* community occupies the older, higher, and more pedologically developed end of the gradient, and bare degraded areas characterize the younger, lower, and less developed end of the gradient. A partially vegetated *Puccinellia-Carex* community occupies an intermediate position. Chapman (1960) proposed a successional sequence in arctic salt marshes from bare mud to a *Puccinellia phryganodes* community, leading to a *Carex subspathacea* community and finally to a *Festuca rubra-Carex glareosa* community. A similar successional gradient from bare algal

mats to *Puccinellia phryganodes*-dominated communities to *Carex salina-Triglochin maritima-Potentilla egedii* communities to *Salix* shrub communities was proposed for James Bay salt marshes by Glooschenko (1980a).

Different successional communities imply a different time since disturbance. A major recent disturbance of all Hudson Bay salt marshes is emergence from Hudson Bay waters. Isostatic uplift in the Hudson Bay Lowlands presently increases salt marsh elevation at a rate between 0.5 and 1.2 cm y^{-1} (Andrews 1970, 1973). Therefore, the 50 to 70 cm difference in elevation between the *Festuca-Calamagrostis* community on the willow edge and the seaward extreme of the salt marsh represents up to 84 years difference in time since emergence from Hudson Bay. In an eastern James Bay marsh, Ringius (1980) estimated the distance between a dense *Salix* community and the seaward extreme of the marsh to represent 106 to 142 years. In a southwestern Hudson Bay salt marsh, a similar distance represents 92 to 122 years (data from Kershaw, 1976, analyzed by Ringius, 1980).

The successional gradient in communities does not follow entirely this simple gradient in time since emergence. Apart from the inland *Festuca-Calamagrostis* zone near the willow edge, the salt marsh is a mosaic (Jefferies 1988 a,b) of different communities. This contrasts with the distinct zonation of temperate and Alaskan salt marshes (Vince and Snow, 1984; Adam, 1990). Active agents in the formation of this mosaic are goose foraging, ice scouring, ice rafting, frost heaving and complex drainage patterns.

Localized and patchy grubbing by geese for graminoid roots in the early spring results in disruption of the top one or more centimeters of the organic layer. Recolonization of small patches c. 1 m^2 is possible, but more extensive areas of disturbance may result in erosion of the organic layer and exposure of the underlying mineral sediments, preventing revegetation (Jefferies, 1988b). This conversion of the *Puccinellia-Carex* community to a bare degraded community is a reversing of direction along the successional gradient.

More extreme erosion may convert the patches to ponds, later to be colonized by

Hippurus-Myriophyllum communities. Pond size may be increased by ice action and intense grubbing and trampling by geese of the pond periphery (Jefferies et al., 1979). In western Alaska, salt-marsh ponds are prevented from being revegetated by members of the *Puccinellia-Carex* community by the salinization of the ground under drying ponds (Mason, 1981).

Summer grazing by geese can slow the successional process. Protection of *Puccinellia-Carex* swards in the upper salt marsh from grazing results in the invasion of dicotyledonous species less tolerant to grazing, an increase in standing crop and the organic layer, and, ultimately, a *Festuca-Calamagrostis* community (Bazely and Jefferies, 1986; Hik et al., 1992). Decreases in soil salinity may also be involved in this transition from a *Puccinellia-Carex* community to a *Festuca-Calamagrostis* community (Bazely, 1984; Bazely and Jefferies, 1986). The successional sequence from a *Puccinellia-Carex* community to a *Festuca-Calamagrostis* community is therefore being delayed by goose grazing. Even when such exclosed sites are re-exposed to grazing this *Festuca-Calamagrostis* community does not revert to a *Puccinellia-Carex* community, at least in the short term (Bazely and Jefferies, 1986; Hik et al., 1992). This suggests that the *Puccinellia-Carex* and *Festuca-Calamagrostis* communities are stable states for the upper salt marsh with successional change between them being alternately accelerated by isostatic uplift and decelerated by goose grazing (Hik et al., 1992).

Other studies have reported that grazing by waterfowl, sheep, or cattle and mowing decelerates successional change (Ranwell, 1968; Bakker, 1978, 1985; Smith, 1983; Joenje, 1985; Jensen, 1985; Adam, 1990). In at least one case, increased surface salinities caused by grazing were responsible for this "resetting" of the successional clock (Joenje, 1985).

In addition to goose grazing, the physical processes of ice scouring, ice rafting and frost heaving also affect vegetation structure. Ice scouring results in a larger scale disturbance of the organic layer, especially in the lower portions of the marsh, and like grubbing results in the conversion of intact swards to bare degraded areas. Ice rafting causes

the redistribution of 5 to 30 cm thick turves of soil, usually under 1 m^2 in area, resulting in patches of different edaphic conditions, and so increases the spatial heterogeneity in communities. Frost heaving results in a instant increase in elevation, which leads to better drained soils, and consequently may cause a *Festuca-Calamagrostis* community to replace a *Puccinellia-Carex* community.

The salt marsh of East Bay flats is more degraded than that of Randy's flats. In part, this may reflect the dryness and height of East Bay vegetation relative to Randy's flats. All flats have a similar slope of ca. 1.2 m km^{-1}, but since the willow edge is further away from the shoreline in the East Bay flats, it, and most of the intact vegetation, is 20 to 40 cm higher than in Randy's flats (Fig. 3.1). The high elevation of the landward end of East Bay flats causes this to be one the first areas to become snow-free in the spring, and consequently intense grubbing occurs in this area (B. Ganter, unpublished data). Higher elevation and lack of freshwater streams or brackish tides may also cause greater soil salinities in East Bay flats than in the other flats. The high elevation also suggests that wind erosion may also be more important on East Bay flats. Grubbing, high soil salinity and erosion all reduce vegetation cover (Chapters 5,7).

CHAPTER 4: PLANT BIOMASS AND SOIL SALINITY

4.1 Introduction

The sediments of most coastal salt marshes become salty through tidal inundation of seawater, and the subsequent concentration of salts by evaporation (Beeftink, 1977). Soil salinities therefore tend to decrease with depth and decrease landward beyond the limit of tidal inundation (Beeftink, 1977; Zahran, 1977). Such a tidal salt source is inconsistent with the situation in many salt marshes of Hudson and James Bays because a) salinity increases with depth (Price and Woo, 1988a,b; Price et al., 1988, Price et al., 1989); b) salinity increases landward in salt marshes (Jefferies et al., 1979; Glooschenko and Martini, 1978; Glooschenko and Clark, 1982; Price et al, 1988), c) halophytic salt marsh vegetation is found landward of tidal limits (Kershaw, 1976; Jefferies et al., 1979; Price and Woo, 1988b; Price et al., 1988), and d) nearshore tidal salinities are so low (c. 4 g dissolved salts/l) that they flush the top sediments of salts (Jefferies et al., 1979; Ewing and Kershaw, 1986; Price and Woo, 1988b; Price et al., 1988; Price et al., 1989). The low salinity of nearshore waters is caused by a substantial outflow of freshwater from surrounding land, as well as the effects of melting snow and ice floes in the spring (Price et al., 1989).

Hudson and James Bay salt marshes receive much of their salts from buried Tyrell Sea marine deposits. The postglacial Tyrell Sea occupied a large portion of the Hudson Bay Lowlands about 8000 years before present, and deposited a layer of blue-grey marine clay up to 56 m thick (Lee, 1960). Subsequent isostatic uplift, retreat of the shoreline seaward, beach building and peat development have resulted in these marine clays being buried under as much as 3 m of sediments (Martini, 1981; Price and Woo, 1988a). Salinity of the pore water of Tyrell Sea sediments is reported to be 21-25 g dissolved salts l^{-1} (Price and Woo, 1988a). Pore waters from surface marsh sediments are isotopically (O^{18} and D) more similar to sea water and deep marine clays, than to inshore tidal water, illustrating the importance of Tyrell Sea sediments in supplying the salt marsh with salts (Price and Woo, 1988a).

Only in areas of Hudson and James Bays where circulation patterns and the absence of freshwater inflows allow tidewater to have a high salinity, does the distribution of vegetation and its species composition reflect tidal limits. At such locations, the salinity of sediments decreases with distance landward and with depth above the Tyrell Sea clays (Price et al., 1989).

Although the work reported above explains large scale (100m-1km) spatial patterns in the soil salinity of Hudson/James Bay salt marshes, relatively little is known about spatial patterns on smaller (1m-10m) scales.

The salt marsh at La Pérouse Bay, Manitoba, has a highly heterogeneous distribution of vegetation, with islands of high biomass *Puccinellia-Carex* swards, bare patches and regions, and intermediate low biomass areas, as described earlier (Chapter 2). This study attempts to relate the salinity of surface sediments to these spatial patterns in vegetation. A key prediction of the positive feedback hypothesis accounting for salt-marsh destruction (Chapter 1) is examined, namely that salinity is inversely related to biomass.

Vegetation could affect soil salinity by modifying evapotranspiration rates. Evapotranspiration from a surface is affected by surface wind speed, air humidity and soil moisture, and the heat flux between surface and air, as described by Penman's combination model and related models (Gay, 1981). Surface wind speed, according to wind profile theory, is decreased as the surface "roughness length" increases. Surface roughness length is higher for vegetated surfaces than unvegetated surfaces (Monteith and Szeicz, 1961; Fuchs, 1979), and higher for densely vegetated surfaces than poorly vegetated surfaces (Seginer, 1974). Vegetation can therefore reduce evaporation from a surface by reducing surface wind speeds (ie. increasing the boundary layer of still air). The presence of vegetation also affects surface albedo (Otterman, 1974; Graetz and Cowan, 1979), and if vegetation reduces the surface albedo relative to that of bare soil, lower soil temperatures and hence lower evaporation rates can occur (eg., Iacobelli and Jefferies, 1991). The presence of organic debris on the soil surface under vegetation may also reduce surface permeability to water

vapour, as has been reported for soil under a 2 to 3 mm mulch layer in arid ecosystems (Moomen and Barney, 1981). Any or all of these effects could reduce evaporation from vegetated surfaces relative to unvegetated areas at La Pérouse Bay.

Evaporation rates at La Pérouse Bay are expected to be highest in mid-summer, when air temperatures are high and relative humidity is low. Differences between vegetated and unvegetated areas in evaporation rate, and hence salinity, are therefore predicted to be greatest on warm, dry mid-summer days.

Other soil variables expected to be influenced by vegetation or evaporation, namely soil redox potential, soil water content, and soil bulk density, are also examined. In *Spartina alterniflora* swards, for example, soil oxidation is greater in high biomass swards than low biomass swards because air entry into the soil is enhanced by high transpiration rates associated with the former (Howes et al., 1986). Graminoid roots may also directly release oxygen into the soil (eg., Wilson, 1993). Lastly, the effect of bare patch size on salinity is examined to determine whether there is a threshold effect on salinity as patch size increases.

4.2 Hypotheses

1) Soil-water salinity is inversely related to plant above-ground biomass (positive feedback hypothesis 1, Chapter 1).
2) Evaporation rates are higher in unvegetated areas than in vegetated areas (positive feedback hypothesis 3, Chapter 1).
3) Differences in evaporation rate between vegetated and unvegetated sites are greatest on warm, dry, mid-summer days (positive feedback hypothesis 7, Chapter 1).
4) Differences in soil-water salinity between vegetated and unvegetated areas are greatest in warm, dry mid-summer periods (positive feedback hypothesis 8, Chapter 1).
5) The size of a bare patch affects soil-water salinity.

4.3 Methods

4.3.1 Study site

All sites were on the eastern salt-marsh of La Perouse Bay (East Bay flats; Fig 3.1) unless otherwise noted. The study area is not covered by tides except in the autumn.

4.3.2 Soil variables and biomass

4.3.2.1 Soil-water salinity.

The salinity of a block of soil can be determined by several methods, and each yields related information (Richards, 1954; Rhoades, 1982). By mixing and incubating soil with a given amount of water, and determining the salinity of the resultant solution after allowing the colloidal mixture to equilibrate, the salinity of both the soil water and a percentage of salts bound to clay particles by weak electrical forces is assayed (Richards, 1954; Rhoades, 1982). In contrast, by inserting pore water sampling tubes into the sediment, the salinity of free flowing pore water is assayed. However, this method is inappropriate and ineffective in dry soils (Rhoades, 1982). When soil water is extracted with pressure (manual, centrifugal, press), solutes and water held in the larger soil pores are removed, but not salts electrically held to clay particles of the matrix (V. Timmer, pers. comm). The latter two methods therefore approximate to the salinity of water adjacent to roots under field conditions, while the first method approximates to the salinity of soil water when the soil has an unnaturally high water content (Rhoades, 1982). In this study, soil water was extracted by pressure in most cases, because the effect of salinity on plant growth under field conditions is of interest. Soils were too dry for use of pore water tubes.

The top centimeter of soil was used in most cases for salinity determinations. *Puccinellia phryganodes* roots are densest in the top 1-2 centimeters of soil, and almost all roots are within the top 5 cm of soil. Salinity conditions of the top centimeter of soil are

therefore an approximate measure of salinity encountered by *Puccinellia* plants.

4.3.2.2 1991 methods

Sites were selected, representing high and low biomass vegetation and bare areas (see Chapter 2 for definitions). Initially, each biomass category was represented by 5 sites, but this was increased to 10-11 sites per category on and after July 2 when it was apparent that there was a large amount of spatial variability in soil salinity. Blocks of soil (approximately 10cm x 10 cm x 3 cm) were collected at random from a c. 50 cm x 50 cm area at each site on June 1, June 10, June 23, July 2, July 10, August 7, and August 31, 1991. This three-month period encompasses all of the snow goose grazing season and most of the graminoid growing season (Bazely and Jefferies, 1989). Maximum snow melt occurred on approximately May 18 in 1991 (B. Ganter, pers. comm.).

Soil water was extracted from the top centimeter of soil on all dates except June 1 and June 10. No soil water was extracted on June 1, and soil water was extracted from the top 4 cm of soil on June 10. Soil profiles indicate that salinity does not change appreciably with depth in the top 4 cm of soil in early June (see results, also Iacobelli and Jefferies, 1991), so the June 10 salinity results are assumed to be directly comparable with those of other dates. On dates prior to July 10, soil water was extracted by compressing the soil manually or by the use of a soil press with a 1.5m lever (depressed c. 30 cm for 30 seconds). By July 10, however, soils had become so dry that centrifugation (described in Chapter 2) was needed to extract soil water. The salinity of soil water extracted from the same soil blocks by both compressing the soil manually and by centrifugation were comparable. Specifically, in a linear regression of centrifugation salinity vs. press salinity, the slope was not significantly different from 1, nor the intercept from 0 (t-tests, $p<0.05$, $n=15$). Irregularities in sample size in 1991 reflect the difficulty in extracting soil water. In all cases, the extracted soil water was diluted, frozen, and later analyzed for sodium (an index of salinity as described later) after thawing and further dilution. An automated flame emission spectrophotometer was used for sodium determinations, calibrated for use between 0.1 and 1.0 mg/l sodium.

Other soil variables may be affected by vegetation, such as soil redox potential, soil water content and soil bulk density, as described earlier. The redox potential (E_h values) of the top 2 cm of each block of soil was determined by the use of a platinum electrode, and, because of the variability of redox values through the soil profile, was recorded as a range of values. The electrode was routinely standardized with ZoBell's solution (Howes et al., 1981), which has an E_h value of +430 mV at 25°C. An approximately 3cm x 4 cm x 1cm deep piece of soil of known dimensions was weighed, dried, and re-weighed. Soils were dried above an oil stove at approximately 50°C for at least 5 days. Bulk density of the soil was calculated as grams of dry soil per cm^3 of wet soil. Water content was calculated as grams of water (ie. $g_{wet\ soil} - g_{dry\ soil}$) per gram of dry soil. This is gravimetric water content; volumetric water content (g H_2O/cm^3 soil) can be calculated as the product of gravimetric water content and bulk density. Most statistical analyses involving gravimetric water content were repeated using the data of volumetric water content, but as there were no appreciable differences between the results, only gravimetric water content of soils is reported here (volumetric water content can be calculated from data supplied in this chapter as described above). Note that bulk density, water content and soil water salinity were all determined on the top centimeter of soil from the same soil block, and so the data can be directly compared.

Above-ground live biomass was clipped from the surface of the same soil blocks on three dates: June 1, July 10, and August 31. Using the same blocks of soil for both biomass and soil analyses ensures that biomass and the soil variables are directly comparable.

4.3.2.3 1992 methods

Twenty sites were selected to represent each category (high biomass, low biomass, bare areas) for a total of sixty sites. Thirty of these sites were from 1991, and thirty additional sites were selected in 1992. Analyzing the same sites for salinity and biomass in 1991 and 1992 permitted between-year comparisons to be made (Chapter 2). The thirty additional sites included twelve (grazed) sites also used for the field demography experiment of 1992 described in Chapter 5. Although the results of soil analyses reported here and in

Chapter 5 are not strictly independent, the overlap is minor. As in 1991, blocks of soil were collected from each site during the growing season, specifically on June 16, June 26, July 12, July 21, and July 30, 1992. The first sampling date was just five days after a rapid melt of a thick snow layer over much of the salt marsh (snow cover decreased from 50% to 5% between June 10 and June 12, 1992; B. Ganter, pers. comm.). On this date only, soil was collected from ten or eleven of the twenty sites in each category; on all other dates soil was collected from all twenty sites.

Soil water was extracted from the top centimeter of soils by centrifugation on all sampling dates in 1992, as described earlier. Sodium concentration of the extracted soil water, and redox potentials, bulk density, and water content of the soils were determined as in 1991.

Above-ground live biomass was clipped from the surface of the soil blocks from ten sites per biomass category on June 16, June 26, and July 30, six sites per category on July 12, and all twenty sites per category on July 21.

4.3.2.4 Statistical methods

In 1991, repeated measurements of sodium concentration in soil water were made for 24 sites (n=7,11,6 for high biomass, low biomass and bare categories, respectively) between July 2 and August 31. Repeated measures for all other soil variables were made for 29 sites (n=10,10,9 for high biomass, low biomass, bare categories, respectively) between July 2 and August 31, 1991. In 1992, repeated measurements of sodium concentration in soil water and other soil variables were made for all 60 sites on all dates except June 16. A repeated measures ANOVA, with sites nested within the categories and crossed by dates, was used to analyze data for 1991 and 1992 (each of sodium concentration in soil water, soil water content, soil redox potential, and soil bulk density) for these sites and dates. Data was transformed when necessary to ensure variances were homogeneous (F_{max} test; Kirk, 1982). Specifically, sodium concentration in soil water and soil water content was log-transformed

in 1991 and 1992, and redox potential was squared in 1991.

Heteroscedasticity could not be reduced in the data of redox potential for 1992 by standard techniques (means uncorrelated with variances) so non-parametric methods were used in lieu of ANOVA. The effect of date, using sites as blocks, was analyzed by the use of a Friedman test (Gibbons, 1985). Although planned comparisons (between sites of different categories) after a significant site effect in a Friedman test (using dates as blocks) could be used to determine the effect of category, this approach could not test for an interaction between dates and category (Miller, 1966). In this case, the interaction was of particular interest. Therefore, the effect of category was analyzed separately for each date by individual Kruskal-Wallis tests (Sokal and Rohlf, 1981). Since these analyses are not independent (sites are the same), the significance level for each test was adjusted by a Bonferroni procedure (Bray and Maxwell, 1985; ie., for an experiment-wise $p<0.05$, $p<0.0125$ for each of 4 tests).

Planned multiple comparisons (see hypotheses) are analyzed by F tests for parametric data, and Wilcoxon rank-sum tests for non-parametric data. Unplanned multiple comparisons are analyzed by the use of Tukey's test for parametric data. Day and Quinn (1989) recommend Tukey's test as the most powerful simultaneous test that controls the experiment-wise error rate. Unplanned comparisons of non-parametric data are performed using the multiple comparison procedure described by Gibbons (1985; p313).

In both 1991 and 1992, there are dates for which data is not available for all sites. These dates are therefore excluded from the above repeated measures ANOVAs. Since data obtained on such dates are not strictly independent from that obtained on later dates (since some sites are the same), individual ANOVAs for such dates would not be independent from repeated measures ANOVA on later dates. Data for these dates are therefore not analyzed statistically, but merely presented in graphical form.

All statistical calculations were made using SAS software (SAS, 1988).

4.3.2.5 Converting sodium concentrations into salinity

The salinity of soil water is the total concentration of dissolved salts in solution, consisting mainly of the cations sodium, calcium, magnesium and potassium, and the anions chloride, sulphate, carbonate, bicarbonate, and nitrate (Richards, 1954). In using sodium concentration as an index of salinity, it is assumed that sodium is a constant proportion of all dissolved ions.

To test this assumption, soil was collected from five sites on June 16 and July 21, 1992, and soil water was extracted by centrifugation. The extracted soil water was later analyzed for sodium, magnesium, calcium and potassium by flame spectrophotometry. Salinity is anticipated to be very low on June 16, just three days after snowmelt, and near peak levels on July 21.

In all sites and on both dates, sodium had the highest concentrations, followed by magnesium (Table 4.1a). On June 16, sodium was, on average, 79.3% of the total concentration of the four cations, magnesium was 10.2%, calcium was 6.8%, and potassium was 3.7%. No site had more than a 2% deviation from these percentages. On July 21, sodium was, on average, 64.0% of the total concentration of the four cations, magnesium was 26.0%, calcium was 6.1%, and potassium was 3.9%. The differences in cation ratios is due to a preferential enrichment of magnesium (Table 4.1b). Between June 16 and July 21, sodium, calcium, and potassium concentrations increased 5-fold, whereas magnesium concentrations increased 15-fold.

Clay particles have an increasing affinity for divalent cations relative to monovalent cations with increasing solute concentration (Shainberg, 1975). This may explain the enrichment of magnesium, although it is then not clear why calcium was not similarly enriched over the season. The opposite trend has also been reported. Increased concentration of dissolved salts through the season can cause the solubility limits of magnesium salts to be

Table 4.1. a. Concentration of major cations in soil water extracted from the soil of five sites on June 16 and July 21, 1992. **b.** Enrichment factors (-fold) of cations between June 16 and July 21 for the same five sites.

a

	Na^+ (g/l)		Mg^+ (g/l)		Ca^+ (g/l)		K^+ (g/l)	
Site	June 16	July 21	June 16	July 21	June 16	July 21	June 16	July 21
1	2.93	21.2	0.376	6.864	0.234	0.764	0.130	1.01
2	6.53	11.5	0.931	3.321	0.654	1.01	0.245	0.608
3	2.71	8.85	0.377	5.547	0.236	1.523	0.132	0.733
4	4.07	9.61	0.498	4.838	0.288	0.975	0.132	0.663
5	1.20	10.8	0.134	3.822	0.107	1.06	0.073	0.630

b

Site	Na^+	Mg^+	Ca^+	K^+
1	1.25	18.27	3.27	7.76
2	1.77	3.57	1.54	2.48
3	3.27	14.71	6.47	5.55
4	2.36	9.70	3.39	4.22
5	9.01	28.49	9.88	8.65
mean	4.73	14.9	4.91	5.73
S.D.	$\pm$2.87	$\pm$8.38	$\pm$2.95	$\pm$2.26

exceeded, resulting in depletion of soluble magnesium relative to sodium (Richards, 1954).

If it is assumed that salinity is directly related to the combined concentrations of sodium, magnesium, calcium, and potassium ions, this enrichment of magnesium over the season would cause a salinity-sodium relationship based on July 21 values to overestimate salinity from sodium concentrations by 16% on June 16. This comparison between snowmelt and peak salinity levels is the most extreme error in estimating salinity from sodium concentrations. As soils dried after the spring melt, the overestimation would be progressively reduced.

Differences between dates in salinity, therefore, may be slightly greater than the sodium values indicate. Within a given date, however, the sodium-salinity relationship appears robust. On July 12, 1992, salinity of extracted soil water was measured with a portable salinity meter, and sodium concentrations of the same soil water was determined by flame spectrophotometry (n=76; salinity range 4 to 68 g dissolved salts/l). A linear regression model of salinity versus sodium concentration (Fig. 4.1) had a strong fit ($r^2=0.96$), and the equation was as follows:

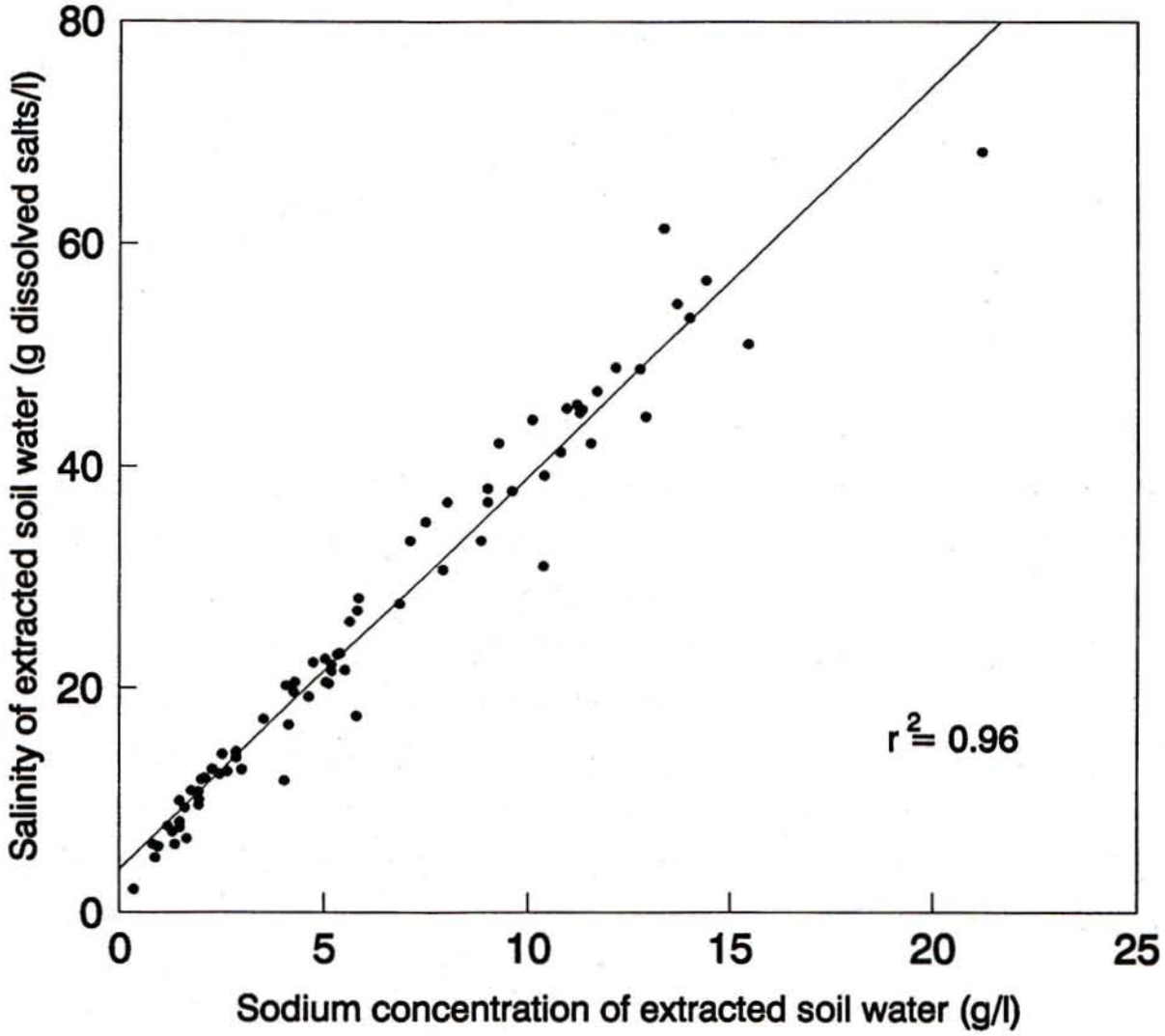
salinity (g diss. solids/l) = 3.519 * Na conc.(g/l) + 3.850

This equation is used to approximate salinity values from sodium values for all dates, although small differences between dates in the sodium-salinity relationship may exist. By using data from July 12, peak summer salinity may be underestimated, and post-melt spring salinity may be overestimated (by less than 16%).

4.3.3 Sodium concentrations in the soil water at different depths in the soil profile

Blocks of soil, from the surface to 8-18 cm deep, were collected from the eastern salt-marsh flats of La Pérouse Bay (East Bay flats; Fig 3.1) on May 31, 1991 and on July 9, 1992. The three blocks of soil collected on May 31 represented high biomass, low biomass,

Fig. 4.1. Salinity of soil water as a function of sodium concentration of soil water on July 12, 1992. Each point represents salinity and sodium measurements made on the same sample of extracted soil water.



and bare areas. The three blocks of soil collected on July 9 represented high biomass, moist bare, and dry bare areas. Soil was also collected by D. Wilson on August 23, 1991 from the southern salt-marsh flats of La Pérouse Bay (Randy's flats; n=3) and from a *Puccinellia-Carex* community inland from these flats (n=3). In all cases, soil was sliced horizontally at depths representing either horizons or at intervals of 1 cm. Soil water was extracted either manually (May 31) or by centrifugation (July 9, August 23), and analyzed for sodium by flame spectrophotometry. Live roots penetrated most soils to c. 5 cm deep, but were concentrated in the top 2 cm. Stones and/or permafrost underlay soils at a depth of c. 10 cm (May 31) to 15-25 cm (July 9), preventing removal of deeper soil.

4.3.4 Evaporation and biomass

Evapotranspiration can be estimated by models incorporating meteorological data and surface characteristics (Gay, 1981) or by energy or water budgeting methods (Evans, et al., 1981). Evapotranspiration can be measured more directly by water loss from lysimeters (removable containers of soil and vegetation sunk into the ground), or by water loss from standard pans multiplied by an empirically determined correction factor (Gay, 1981). Such standard techniques yield values which can be compared to other studies. In this study, however, only relative values were of interest (ie., the difference between vegetated and unvegetated areas). Furthermore, evaporation from standard pans or modelling techniques integrate evapotranspiration over a large landscape, and are unsuitable for small-scale differences in evapotranspiration (R. Bello, pers. comm.). A non-standard technique involving the measurement of water loss from small tubes sunk in the soil was therefore used. Note that this technique measures direct evaporation, not evapotranspiration (Shawcroft and Gardner, 1983).

Sites were selected in which high biomass swards were adjacent to bare areas in both the eastern and southern salt marshes of La Pérouse Bay. In each of the swards and the bare areas, ten 1.5 ml microcentrifuge tubes (39 mm long, 9 mm inside diameter in top 20 mm, tapering to 5 mm diameter at bottom) were pressed into the ground until the tops were flush

with the surface, and the lids bent back. Each tube was previously filled with 1.5 ml of deionized water, and weighed to the nearest 0.001 g. Tubes were left in the soil until approximately 0.3 to 0.5 g of water had evaporated from the tubes in bare areas. This took 48 hours for tubes sunk in the soil on July 27 and July 31, and only 24 hours for those sunk in the soil on August 3. Tubes were then reweighed, and the amount of water lost by evaporation obtained by subtraction. Three sites were selected on each date at various locations around La Perouse Bay. Tubes in two sites in the southern salt marsh were accidentally filled by tidal inundation on July 27. Since there were then an unequal number of sites for each date, a two-way ANOVA of site ($k=7$) vs. treatment was computed, rather than a three-way site vs. date vs. treatment ANOVA. The effect of date is examined as a planned comparison; this and all other planned comparisons (see hypotheses) are examined by the use of F tests. Data are expressed as μl water lost per hr and are log-transformed to conform to ANOVA assumptions.

4.3.5 Bare patch size and salinity

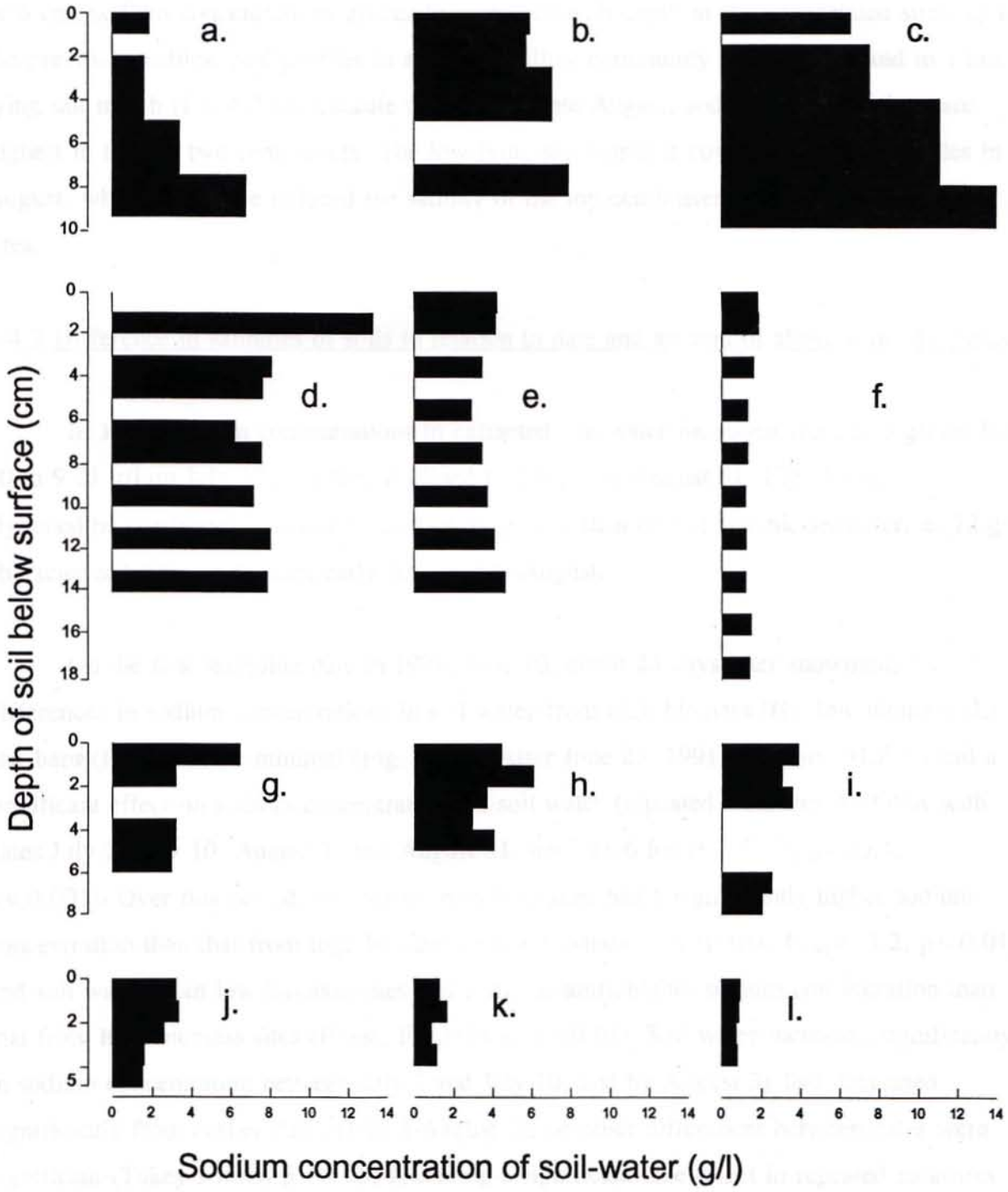
Bare patches in high biomass *Puccinellia phryganodes* vegetation of 10, 30 and 100 cm diameter were selected from an area of the eastern salt marsh in a haphazard fashion, and soil removed from each ($n=5$ patches/size class). Soil water was extracted from the top centimeter by centrifugation, and sodium concentrations were determined by flame spectrophotometry, as described earlier. Data were normally distributed (Shapiro-Wilk's test, $p>0.05$) and variances homogeneous (Bartlett's test, $p>0.05$). Since the type of relationship between patch size and salinity was not predicted (see hypotheses), unplanned comparisons (Tukey's tests) are appropriate.

4.4 **Results**

4.4.1 Sodium concentrations in soil water at different depths in the soil profile.

Two weeks after melt, sodium concentrations in extracted soil water increased with

Fig. 4.2. Sodium concentration of soil water extracted at various depths in the soil profile. Soil was collected on either May 31, 1991 (a-c), July 9, 1992 (d-f), or August 23, 1991 (g-l) in a salt marsh not affected by tides in most of the summer (a-f), in a vegetated inland willow area, also not affected by tides (g-i), and in a vegetated area of an intertidal low-lying salt marsh (j-l). Within the non-tidal salt marsh, soil was from high biomass sites (c,f), a low biomass site (b), an average bare site (a), a dry bare site (d), and a moist bare site (e).


a.
b.
c.
d.
e.
f.
g.
h.
i.
j.
k.
l.
Depth of soil below surface (cm)
Sodium concentration of soil-water (g/l)

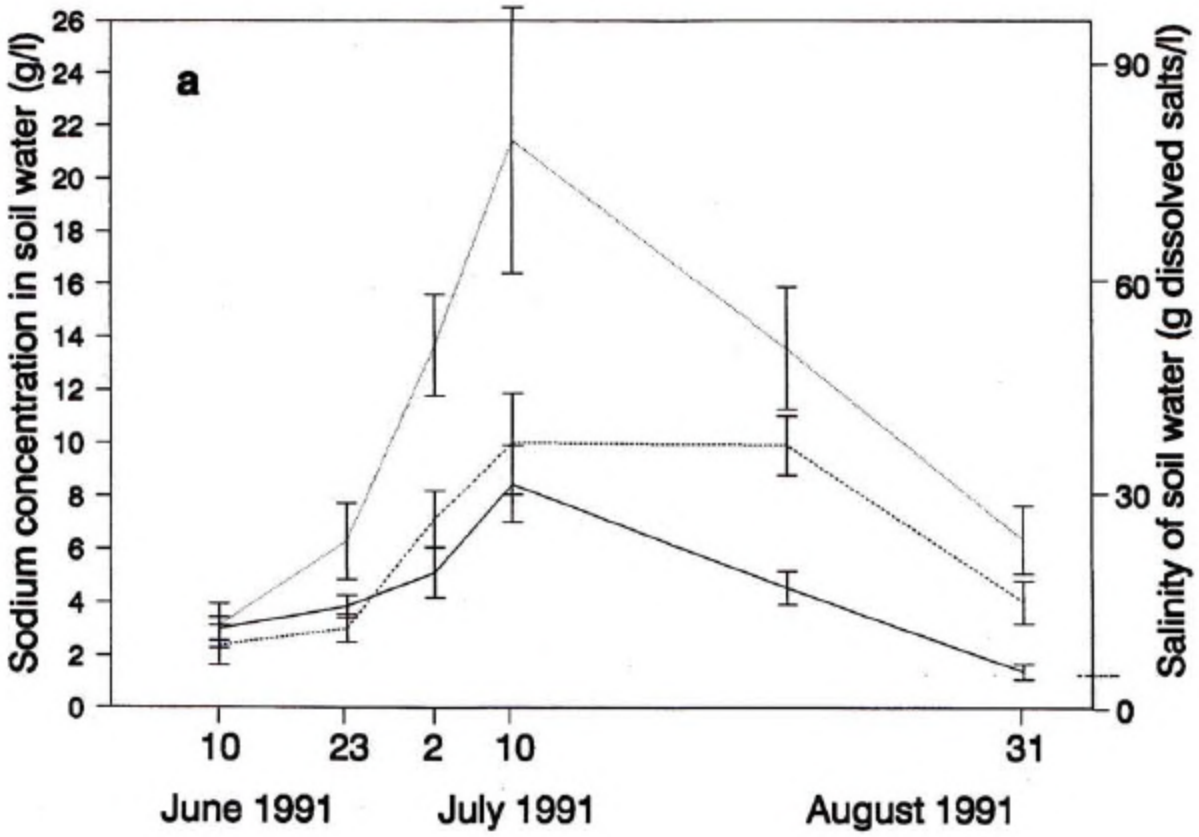
depth to at least 10 cm deep (Fig 4.2.a-c). Within a month after melt, this trend was reversed (Fig 4.2.d-f). High sodium concentrations occurred in the top 2 cm, especially in the unvegetated sites, and decreased with depth down to a depth of ca. 6 cm. Below a depth of 6 cm, sodium concentrations gradually increased with depth in the unvegetated sites, as in the previous profiles. Soil profiles in a nearby willow community (Fig 4.2.g-i) and in a low-lying salt marsh (Fig 4.2.j-l) indicate that even in late August, sodium concentrations are highest in the top two centimeters. The low-lying salt-marsh is covered by brackish tides in August, which may have reduced the salinity of the top centimeter in the profiles at these sites.

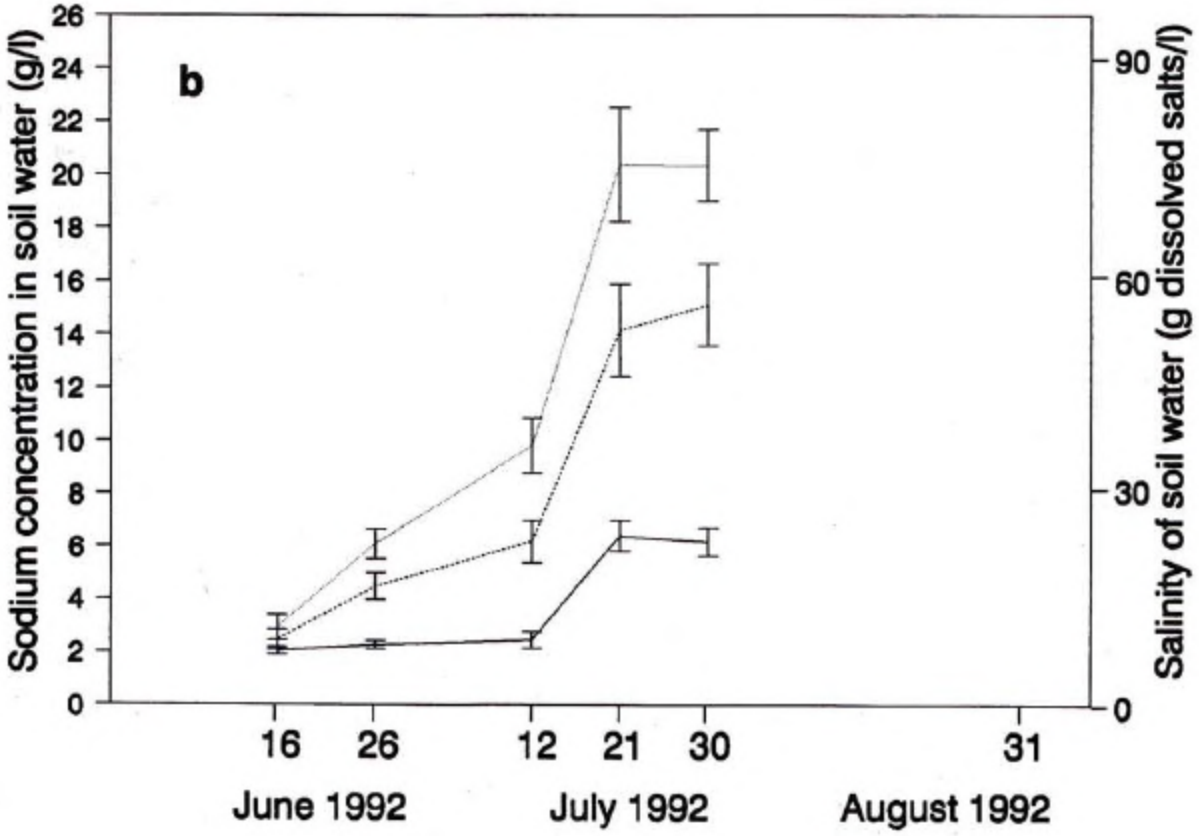
4.4.2 Difference in salinities of soils in relation to date and amount of above-ground biomass

In 1991, sodium concentrations in extracted soil water increased from c. 3 g/l on June 10 to 9-21 g/l on July 10, and then declined to 2-6 g/l by August 31 (Fig. 4.3.a). Hypersaline conditions (sodium concentration greater than that of oceanic seawater, c. 12 g/l) characterized bare areas from early July to mid-August.

On the first sampling date in 1991, June 10, about 23 days after snowmelt, differences in sodium concentrations in soil water from high biomass (H), low biomass (L) and bare (B) sites were minimal (Fig. 4.3.a). After June 23, 1991, category (H,B,L) had a significant effect on sodium concentrations in soil water (repeated measures ANOVA with dates July 2, July 10, August 7, and August 31, n=7,11,6 for H,L,B, $F_{2,20}=10.4$, $p<0.001$). Over this period, soil water from bare sites had a significantly higher sodium concentration than that from high biomass or low biomass sites (F test, $F_{1,60}=33.2$, $p<0.01$), and soil water from low biomass sites had a significantly higher sodium concentration than that from high biomass sites (F test, $F_{1,60}=14.4$, $p<0.01$). Soil water increased significantly in sodium concentration between July 2 and July 10, and by August 31 had decreased significantly from earlier dates (July 2-August 7); no other differences between dates were significant (Tukey's tests, $p<0.05$, following a significant date effect in repeated measures ANOVA, $F_{3,60}=33.4$, $p<0.0001$). Lastly, there was a significant interaction between

Fig. 4.3 Sodium concentration in extracted soil water in 1991 (a) and 1992 (b) in sites representing three biomass categories: high biomass (solid lines), low biomass (dashed lines), and bare sediment (dotted lines). Salinity was not measured directly, but estimated from sodium concentrations as described in the text. Error bars are $\pm$ 1 SE.


a
Sodium concentration in soil water (g/l)
Salinity of soil water (g dissolved salts/l)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
0
30
60
90
10
23
2
10
31
June 1991
July 1991
August 1991


b
Sodium concentration in soil water (g/l)
Salinity of soil water (g dissolved salts/l)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
0
30
60
90
16
26
12
21
30
31
June 1992
July 1992
August 1992

category (H,L,B) and date ($F_{6,60}=2.58$, $p<0.05$). Low biomass sites were more similar in salinity to high biomass sites than bare sites in July, but were more similar in salinity to bare sites than high biomass sites in August (Fig. 4.3, a).

In 1992, trends were similar. Sodium concentration of soil water, extracted from soils newly exposed by melting snow, averaged 0.7 g/l on June 8 (n=6; soil frozen 5 cm below surface). Sodium concentrations in extracted soil water increased in all categories (H,L,B) from c. 2.5 g/l on June 16 to 6-20 g/l in late July (Fig. 4.3.b). Both low biomass and bare sites were, on average, hypersaline on July 21 and July 30. On June 16, just five days after snowmelt, there were no apparent differences in sodium concentrations in soil water between the categories (H,L,B). On later dates, category (H,L,B) had a significant effect on sodium concentrations in soil water (repeated measures ANOVA with dates June 26-July 30, $F_{2,57}=39.86$, $p<0.001$, n=20/category/date). Soil water from bare sites had a significantly higher sodium concentration than that from high or low biomass sites (F test, $F_{1,57}=70.3$, $p<0.001$), and low biomass sites have significantly higher sodium concentrations than high biomass sites (F test, $F_{1,57}=9.0$, $p<0.005$). Differences in sodium concentration in soil water between these dates (June 26-July 30) were also significant ($F_{3,171}=63.45$, $p<0.0001$), with increases between June 26 and July 12 (Tukey's test, $p<0.01$) and between July 12 and July 21 (Tukey's test, $p<0.01$). There was no significant difference between the sodium concentration in soil water in July 21 and July 30, or for any other pair of dates (Tukey's test, $p>0.05$). The interaction between date and biomass category was just significant ($F_{6,171}=2.21$, $p<0.045$). Differences in salinity between bare and high biomass sites are accentuated over the season: the increase in sodium concentration in soil water from bare sites in July relative to that from high biomass sites on June 26 is significantly greater than the comparable increase in sodium concentrations in soil water from high biomass sites in July relative to that from bare sites on June 26 (F test, $F_{1,171}=7.53$, $p<0.05$). The interaction term can be decomposed into no further significant and orthogonal contrasts (F $test_{5,171}$, $p>0.05$).

4.4.3 Differences in other soil variables in relation to date and amount of above-ground biomass

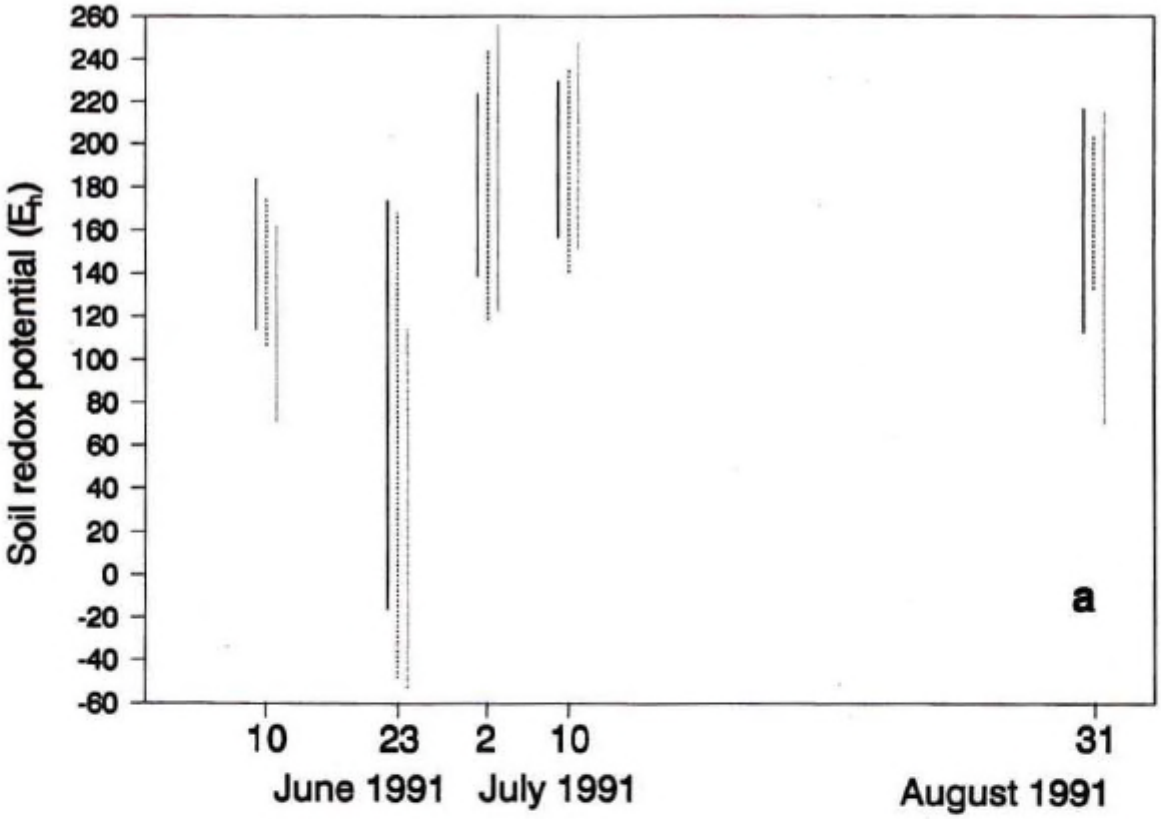
In 1991, the water content of soils decreased from an average of 1.26 $g_{water}/g_{dry\ soil}$ on June 1 (n=15) to 0.72 $g_{water}/g_{dry\ soil}$ on July 10 (n=31), and then increased by August 31 (n=31) to 1.13 $g_{water}/g_{dry\ soil}$ (Fig. 4.4.b; means of all sites). Soil water content did not differ significantly between categories (H,B,L) between July 2 and August 31 (repeated measures ANOVA, n=10,10,9 for H,L,B, $F_{2,11}=0.37$, $p>0.05$) but a date by category interaction was significant ($F_{4,52}=2.89$, $p<0.05$). High biomass sites tended to have wetter soil than low biomass sites in July but the reverse trend occurred on August 31. Soil water content was significantly different between these dates (July 2, July 10, August 31, Tukey's tests, $p<0.01$, after a significant date effect in repeated measures ANOVA, $F_{2,52}=202$, $p<0.0001$).

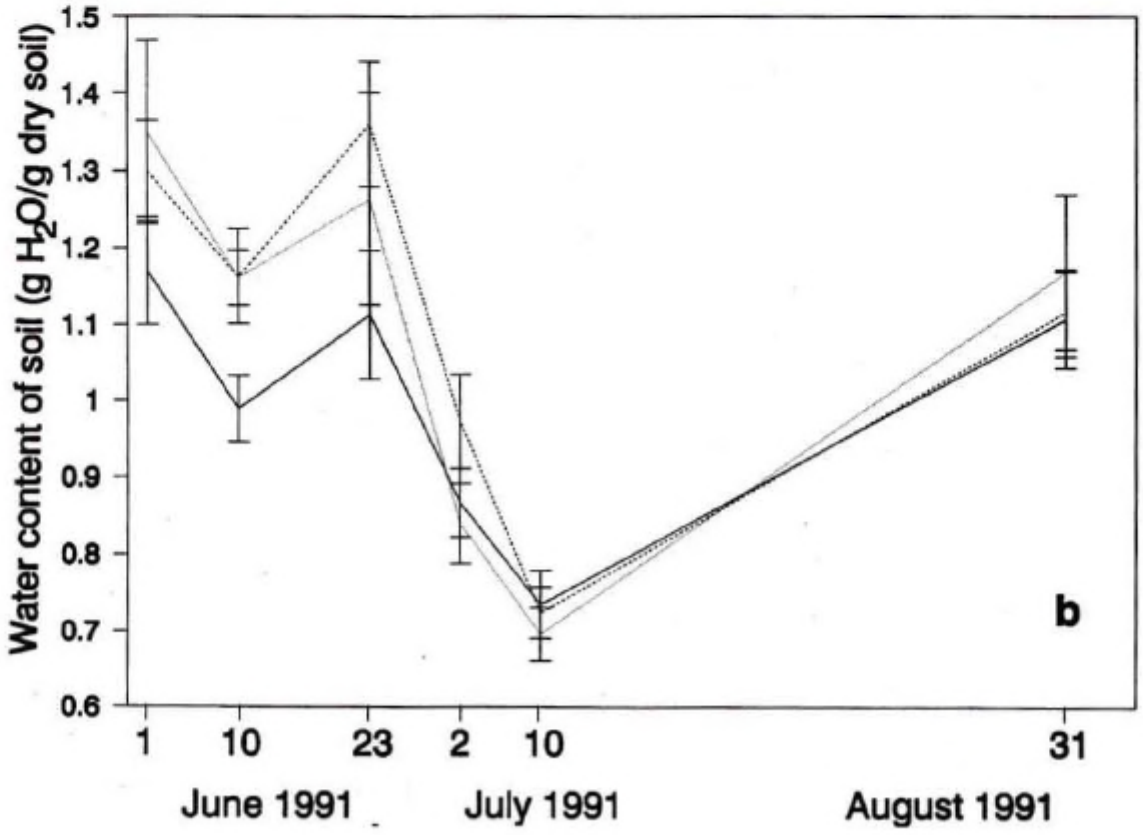
In 1992, water content decreased from an average of 1.34 $g_{water}/g_{dry\ soil}$ on June 16 (n=31) to 0.66 $g_{water}/g_{dry\ soil}$ by July 30 (n=60; Fig. 4.4.d). Repeated measurements of water content in sites between June 26 and July 30 indicated a highly significant effect of date (repeated measures ANOVA, $F_{3,171}=265$, $p<0.0001$, n=20/category/date), with no significant date by category interaction ($F_{6,171}=1.81$, $p>0.05$). Again, there were no significant differences between categories (H,L,B) in water content on these dates (repeated measures ANOVA, $F_{2,57}=0.80$, $p>0.05$).

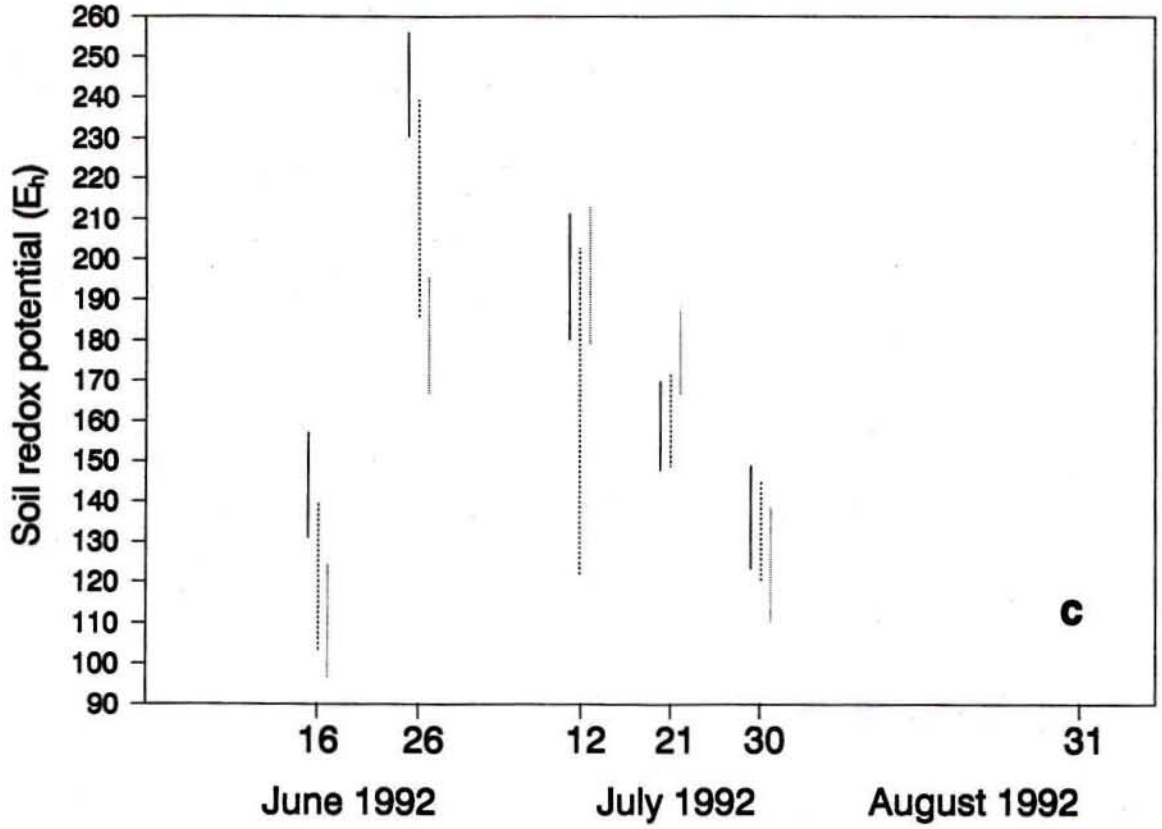
Although differences between biomass categories in water content were, in general, not significant in either 1991 or 1992, both years show a tendency for bare sites to be wetter than high biomass sites for a few weeks after melt, and then for high biomass sites to be wetter than bare areas (Fig 4.4.b,d). In 1991, this reversal occurred about June 10, and in 1992 it occurred in late June to early July.

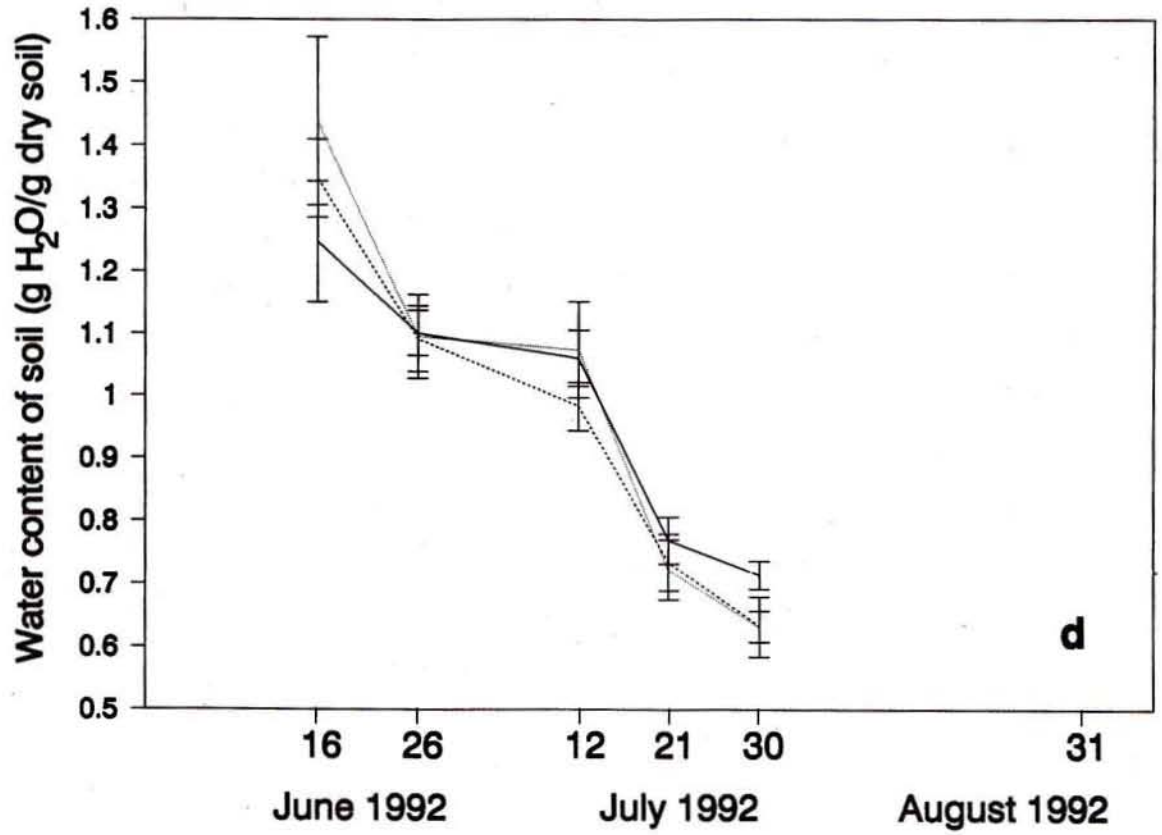
Redox potentials of soils were recorded as a range, and so can be characterized by three values: maximum, minimum, and midpoint ((minimum+maximum)*0.5). Only

Fig. 4.4. Soil redox potential (a,c) and gravimetric water content (b,d) in 1991 (a,b) and 1992 (c,d) in sites representing three biomass categories: high biomass (solid lines), low biomass (dashed lines), and bare sediment (dotted lines). Redox potentials were recorded as a range for each soil sample, so the mean maximum value and mean minimum value are shown, joined by a bar, for each category and date (the length of the bar therefore represents the average range of redox potentials for the appropriate soil samples). Note that horizontal axes are identical in all figures. Error bars for soil water content are $\pm$ 1 SE.


Soil redox potential (E_h)
260
240
220
200
180
160
140
120
100
80
60
40
20
0
-20
-40
-60
a
10
23
2
10
31
June 1991
July 1991
August 1991


Water content of soil (g H_2O/g dry soil)
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
b
1
10
23
2
10
31
June 1991
July 1991
August 1991


Soil redox potential (E_h)
260
250
240
230
220
210
200
190
180
170
160
150
140
130
120
110
100
90
c
16
26
12
21
30
31
June 1992
July 1992
August 1992


Water content of soil (g H_2O/g dry soil)
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
d
16
26
12
21
30
31
June 1992
July 1992
August 1992

midpoint values are analyzed; minimum and maximum values are illustrated in Fig. 4.4.a and 4.5.a.

In 1991, redox potentials of soils were, in general, lowest on June 23, increased by c. 100 mV by late June and then decreased to spring levels by Aug 31 (Fig. 4.4.a). There were no significant differences in midpoint redox potentials between categories (H,L,B) in July and August, 1991 (repeated measures ANOVA, n=10,10,9 for H,L,B, $F_{2,26}=0.00$, $p>0.05$), nor was there a significant category by date interaction ($F_{4,52}=1.37, p>0.05$). Soils were significantly more oxidized in July than in August; no other comparisons between these dates are significant at a 5% level (Tukey's tests, $p<0.01$, after a significant effect of date in repeated measures ANOVA, $F_{2,52}=9.89$, $p<0.001$).

In 1992, redox potentials were lowest on June 16, increased by c. 100 mV on June 26, and then decreased to spring levels by July 30 (Fig. 4.4.c). Repeated measures of midpoint redox potentials in soils between June 26 and July 30 indicated a highly significant effect of date (Friedman test, $p<0.0001$). All differences between these dates were significant (unnamed multiple comparison test described by Gibbons, 1985, p313; $p<0.05$). Within each date (June 26 to July 30), the effect of category was only significant on June 26 and July 21 (Kruskal-Wallis tests on each date, experiment-wise $p<0.05$). Compared to soils from bare sites, soils from high biomass and low biomass sites were more oxidized on June 26, but more reduced on July 21 (Wilcoxon rank-sum test, planned comparison, experiment-wise $p<0.05$). Differences in soil redox potential between high biomass and low biomass sites were not significant on either date (Wilcoxon rank-sum test, planned comparison, experiment-wise $p>0.05$).

In both 1991 and 1992, soils of bare sites tended to be more reduced than those of high biomass sites soon after melt (ie., June 10, 1991, and June 10 and 26, 1992), but then became as or more oxidized than those of high biomass and low biomass sites as the season progressed. This is similar to trends described earlier for soil water content.

Bulk density of soils showed complex trends over the 1991 season (Fig. 4.5.a). Repeated measures of soil bulk density between July 2 and August 31, 1991, indicated higher bulk density on August 31 but no significant difference between July 2 and 10 (Tukey's tests, $p<0.05$, after significant date effect, repeated measures ANOVA, n=10,10,9 for H,L,B, $F_{2,52}=6.70$, $p<0.005$). Although there was no difference between categories ($F_{2,26}=0.75$, $p>0.05$) in soil bulk density, there was a significant date by treatment interaction ($F_{4,52}=3.41$, $p<0.05$, Fig 4.5.a).

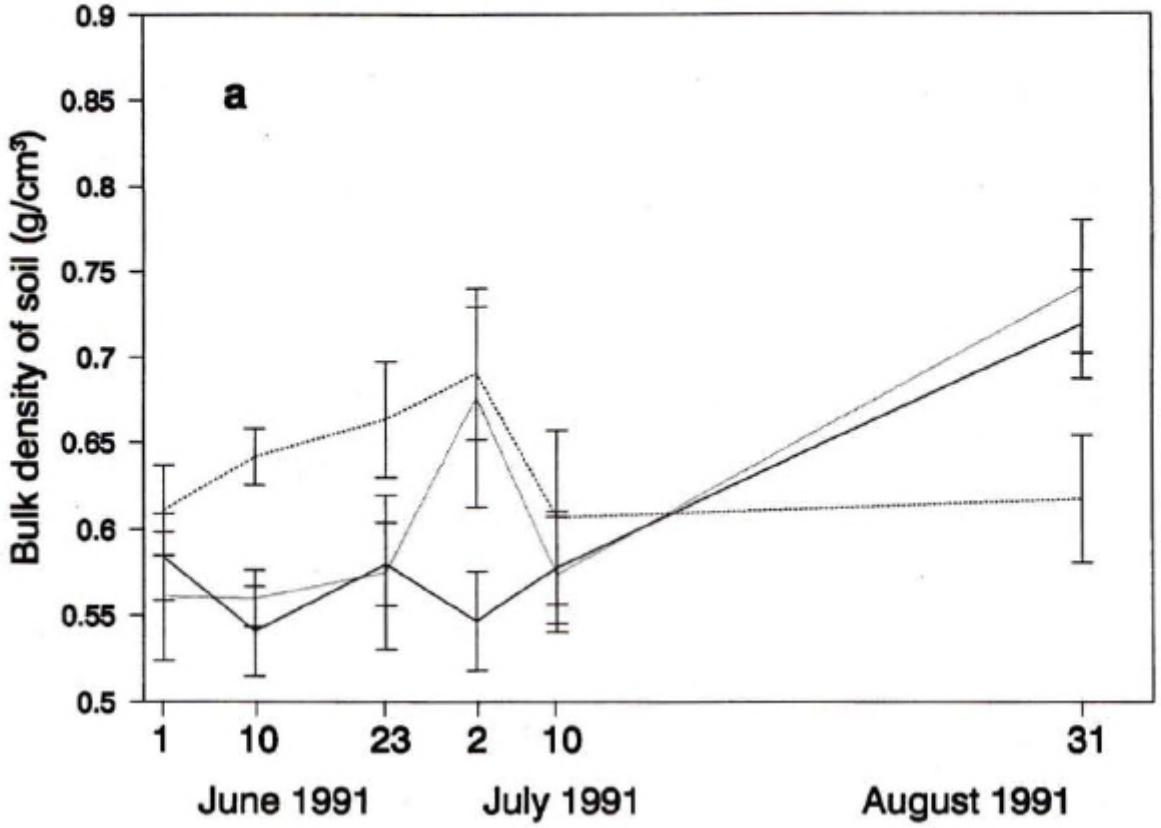
In 1992, soil bulk density increased linearly from June 16 to July 30 (Fig 4.5.b). Repeated measurements of bulk density between June 26 and July 30, 1992, indicate a highly significant date effect (repeated measures ANOVA, n=20/category, $F_{3,171}=16.60$, $p<0.0001$, n=20) but no significant effect of category ($F_{2,57}=1.06$, $p>0.35$), or of a category by date interaction ($F_{6,171}=1.75$, $p>0.10$). Although soil bulk density tended to increase between June 26 and July 30, only the increase between July 12 and July 21 was significant (Tukey's tests, $p<0.05$).

In short, there were clear temporal trends in soil bulk density in 1992 but not 1991. Lower sample size or less precise measurements of soil dimensions in 1991 compared to 1992 may be responsible for this difference.

4.4.4 Relationships between soil variables and biomass

Water content was significantly correlated with sodium concentrations of soil water in all measurements in 1991 ($r=-0.404$, $p<0.0001$, n=114) and 1992 ($r=-0.526$, $p<0.0001$, n=271). Weaker correlations existed between sodium concentration and other soil variables (Table 4.2). Water content was highest on dates with low sodium concentrations, and vice versa, in both 1991 and 1992 (Fig 4.6). On mid-season dates, when sodium concentrations in soil water were greatest in bare sites, intermediate in low biomass sites, and lowest in high biomass sites, mean water content of soils tended to show the reverse trend (even though differences between categories in water content were in general not significant, section

Fig. 4.5. Bulk density of soils in 1991 (a) and 1992 (b) in sites representing three biomass categories: high biomass (solid lines), low biomass (dashed lines), and bare sediment (dotted lines). Error bars are $\pm$ 1 SE.


a
Bulk density of soil (g/cm³)
0.9
0.85
0.8
0.75
0.7
0.65
0.6
0.55
0.5
1
10
23
2
10
31
June 1991
July 1991
August 1991

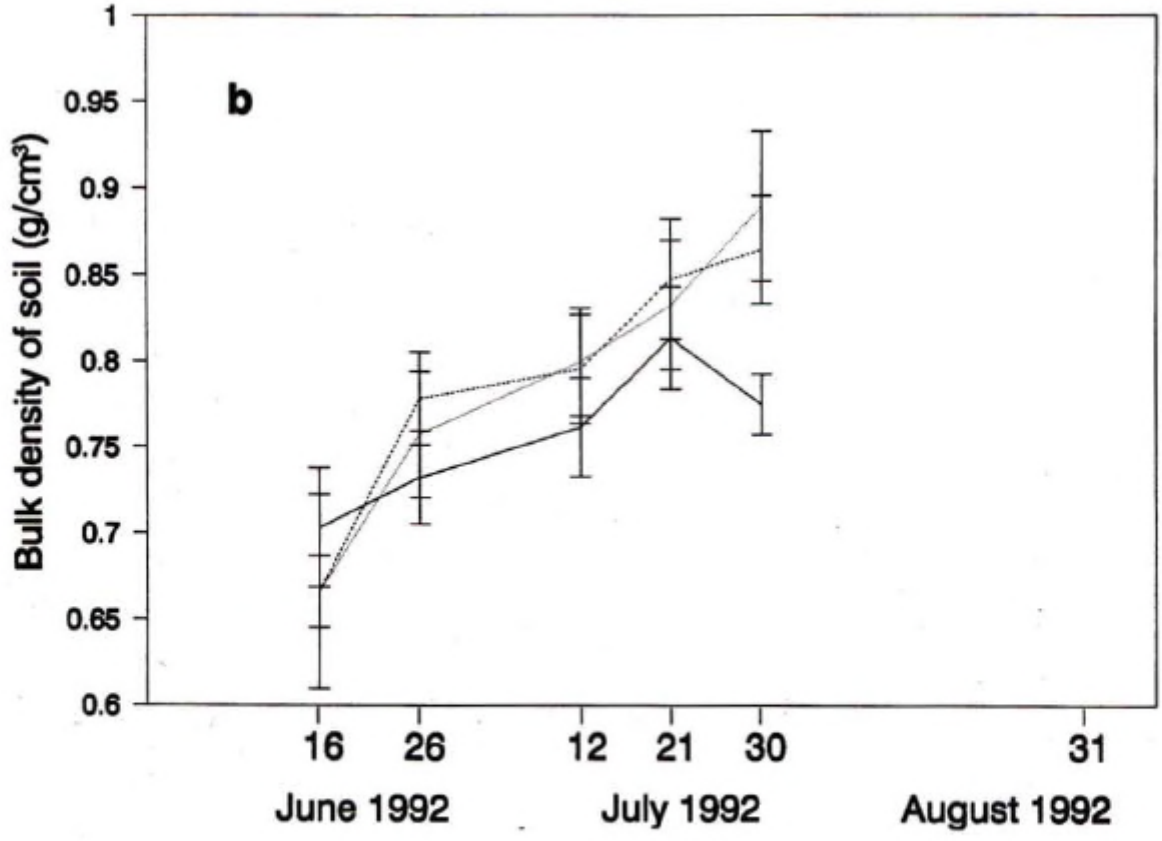

b
Bulk density of soil (g/cm³)
1
0.95
0.9
0.85
0.8
0.75
0.7
0.65
0.6
16
26
12
21
30
31
June 1992
July 1992
August 1992

Table 4.2. Correlation coefficients between sodium concentration in soil water and other soil variables and biomass. Only data for dates on which biomass was measured are shown. Note that within dates, biomass is more strongly correlated with sodium concentration than any soil variable. When data is pooled over dates, the importance of biomass decreases (at least in 1992; biomass was not measured on all dates in 1991, so this correlation coefficient could not be calculated). This indicates that spatial, but not seasonal, trends in soil salinity are determined by biomass.

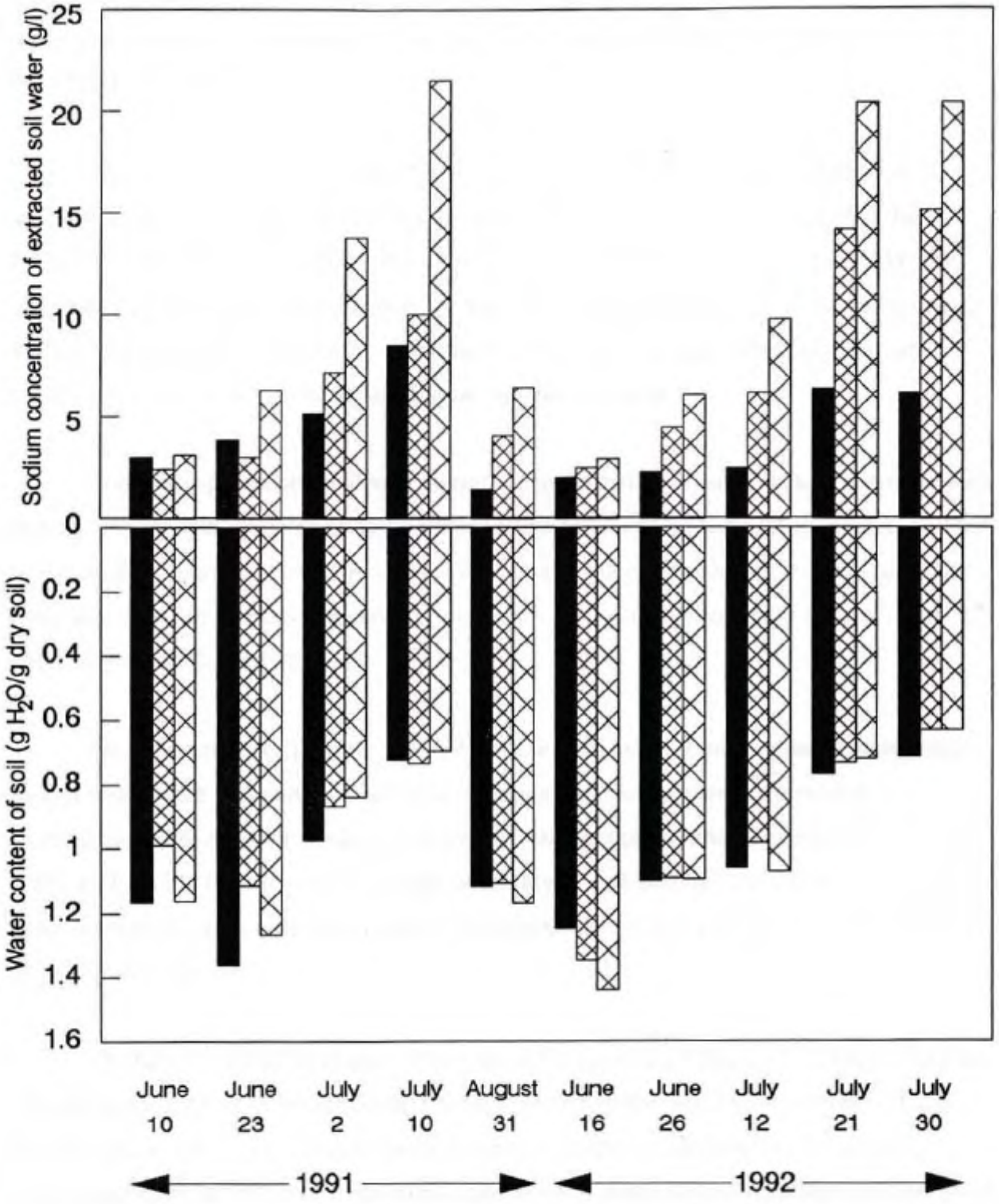
	July 10 1991	August 31 1991	June 16 1992	June 26 1992	July 12 1992
Biomass	-0.35[1]	-0.53*	-0.37[1]	-0.57****	-0.64****
Water content	+0.00	+0.10	+0.10	-0.16	-0.18
Bulk density	+0.08	+0.04	-0.17	+0.24	+0.24
Redox midpoint	-0.09	+0.17	-0.22	-0.16	+0.01
n	31	31	31	60	60

(cont.)

	July 21 1992	July 30 1992	all dates 1991	all dates 1992
Biomass	-0.62****	-0.72****	----	-0.39****
Water content	-0.28*	-0.40**	-0.40****	-0.53****
Bulk density	+0.24	+0.53****	-0.08	+0.41****
Redox midpoint	+0.04	-0.35**	+0.29**	-0.22**
n	60	60	114	271

[1] $p<0.10$; * $p<0.05$; ** $p<0.01$; **** $p<0.0001$.

Fig. 4.6. Seasonal trends in sodium concentration of extracted soil-water and water content of soils in 1991 and 1992 in high biomass sites (solid bars), low biomass sites (bars with narrow cross-hatching), and bare sites (bares with wide cross-hatching). Each bar represents mean values. Note that sodium concentration in soil-water is highest on dates when water content is lowest, and on several mid-summer dates sodium concentration in soil-water is inversely related to water content. Data is identical to that displayed in Figs. 4.3, 4.4, and 4.5.


Sodium concentration of extracted soil water (g/l)
25
20
15
10
5
0
Water content of soil (g H_2O/g dry soil)
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
June 10
June 23
July 2
July 10
August 31
June 16
June 26
July 12
July 21
July 30
1991
1992

4.4.3). Correlations between sodium concentration in soil water and water content were significant only on mid-summer dates with a large sample size (July 21, 1992: r=-0.276; July 30, 1992; r=-0.397).

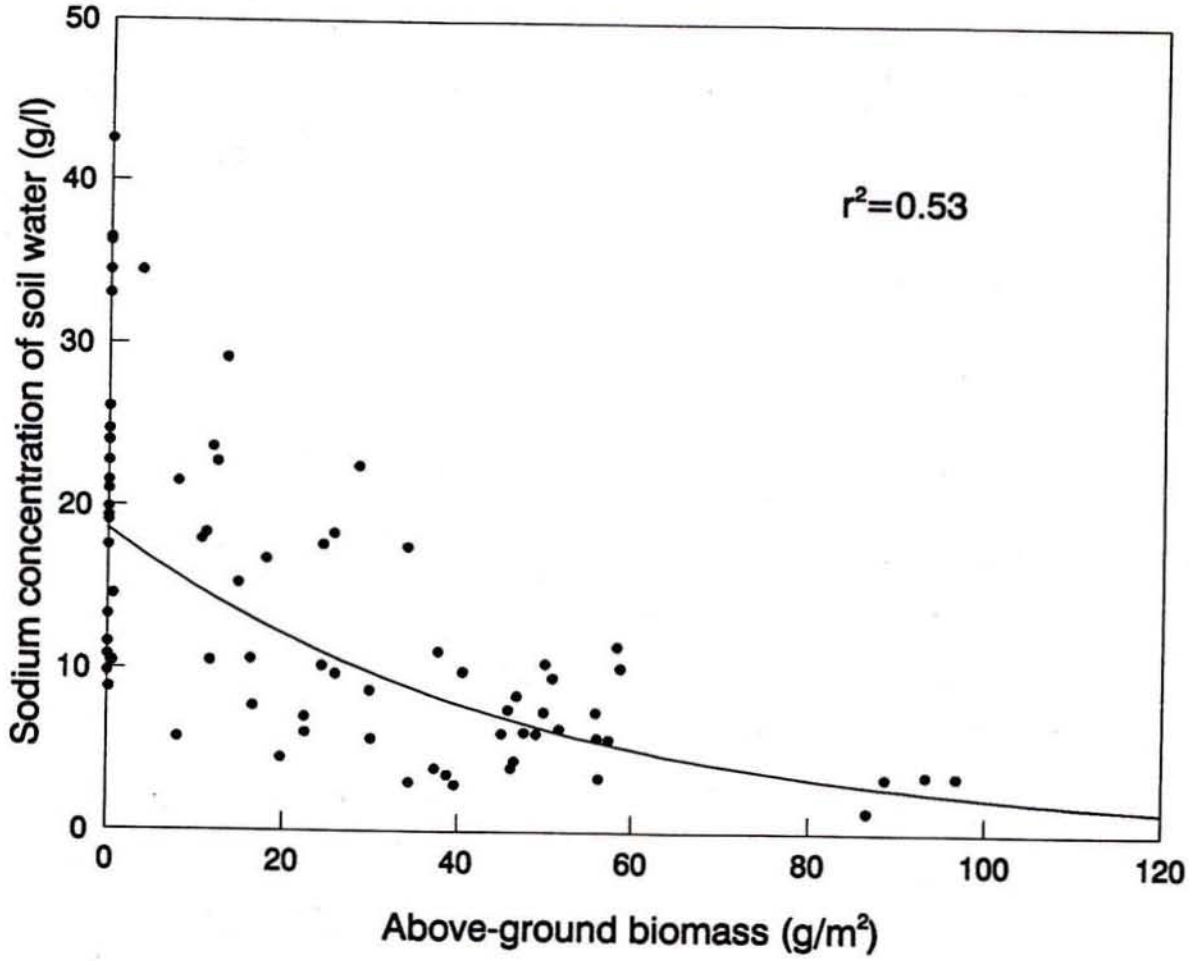
Water content was significantly and negatively correlated with bulk density on all dates in 1991, except June 23 and July 10 (June 1: r=-0.951; June 10: r=-0.902; July 2: r=-0.500; August 31:r=-0.513) and on all dates in 1992 (r from -0.782 to -0.893). This indicates that the surface soils swell when wet, and shrink when dry. Note that bulk density compares the weight of dry soil to the volume of wet soil. Trends in bulk density can therefore be seen as a confirmation of trends in water content.

Soil redox potentials (midpoint) were not correlated with either water content or bulk density on any dates in 1991 or early 1992. In late July, 1992, the driest soils were also the most oxidized (correlation between water content and midpoint redox: r=0.455, July 21; r=0.401, July 30) and the most dense (correlation water content and bulk density: r=-0.477, July 21; r=-0.455, July 30).

On all seven dates in 1991 and 1992 where both biomass and sodium concentrations in soil water were measured, sodium concentration was more strongly correlated with biomass than any of water content, bulk density, and midpoint redox potential (Table 4.2). Only on July 10, 1991 (a date with high variability in soil salinity) and June 16, 1992 (just after snow melt) were correlations between biomass and sodium concentration not significant ($0.10 > p > 0.05$).

On July 21, 1992, biomass at 74 sites (including demographic sites; Chapter 5) was measured, in addition to sodium concentrations of soil water, soil redox potentials, bulk density and water content. In a stepwise regression model (p enter=0.10) of sodium concentration vs. all the above variables, only biomass was included (exponential regression, Fig. 4.7).

Fig. 4.7. Sodium concentration of soil-water as a function of the above-ground biomass of sites on July 21, 1992. The regression line shown was calculated by using an exponential form of biomass.



4.4.5 Evaporation and biomass

Evaporation was measured in a total of seven sites, including three sites beginning on July 27, 1992, one site beginning on July 31, 1992, and three sites beginning on August 3, 1992. In all sites, evaporation rates in unvegetated areas were greater than in vegetated areas (Fig. 4.8). The increase in evaporation from unvegetated areas relative to that from vegetated areas varied from 28% to 155%, and was particularly apparent in site begun on August 3. The effect of vegetation was highly significant (ANOVA, $p<0.0001$). Site effects, as well as the vegetation by site interaction, were also highly significant (ANOVA, $p<0.0001$). Multiple comparison procedures indicate that most of the between site variation can be explained by differences between dates (F tests, $F_{1,125}>60.6$ $p<0.0001$) and by a significantly higher evaporation rate of one site relative to the other two sites of July 27 (F test, $F_{1,125}=14.0$, $p<0.0003$); no other orthogonal comparisons were significant.

The interaction between site and treatment is of interest. Differences in evaporation rate between vegetated and unvegetated areas increased with mean temperature (Table 4.3, Fig. 4.8). Specifically, this differences was greatest in sites begun on August 3 (these sites experienced high temperatures) and lowest in the sites begun on July 31 (this site experienced low temperatures). Most of the interaction term can be explained by such an increase in the difference between treatments with temperature (F tests, $p<0.01$; 62% of interaction SS explained).

4.4.6 Bare patch size and soil salinity

Sodium concentrations in extracted soil water increased with patch diameter (10 cm mean=10.1 ppt; 30 cm mean=10.8; 100 cm mean=18.2 ppt). The patch size effect was significant (ANOVA, $p<0.025$). Specifically, the 100 cm diameter patches had significantly higher sodium concentrations in soil water than the 30 and 10 cm diameter patches (Tukey's tests, $p<0.05$), but there was no significant difference between the 30 and 10 cm diameter patches (Tukey's test, $p>0.05$).

Fig. 4.8. Rate of water loss from small tubes pressed into the sediment in adjacent unvegetated and vegetated areas in each of several sites in the salt-marsh (each site occupies a different position on the horizontal axis) and on several dates in 1992. Error bars are $\pm$ 1 SE and are not shown where smaller than the symbol.

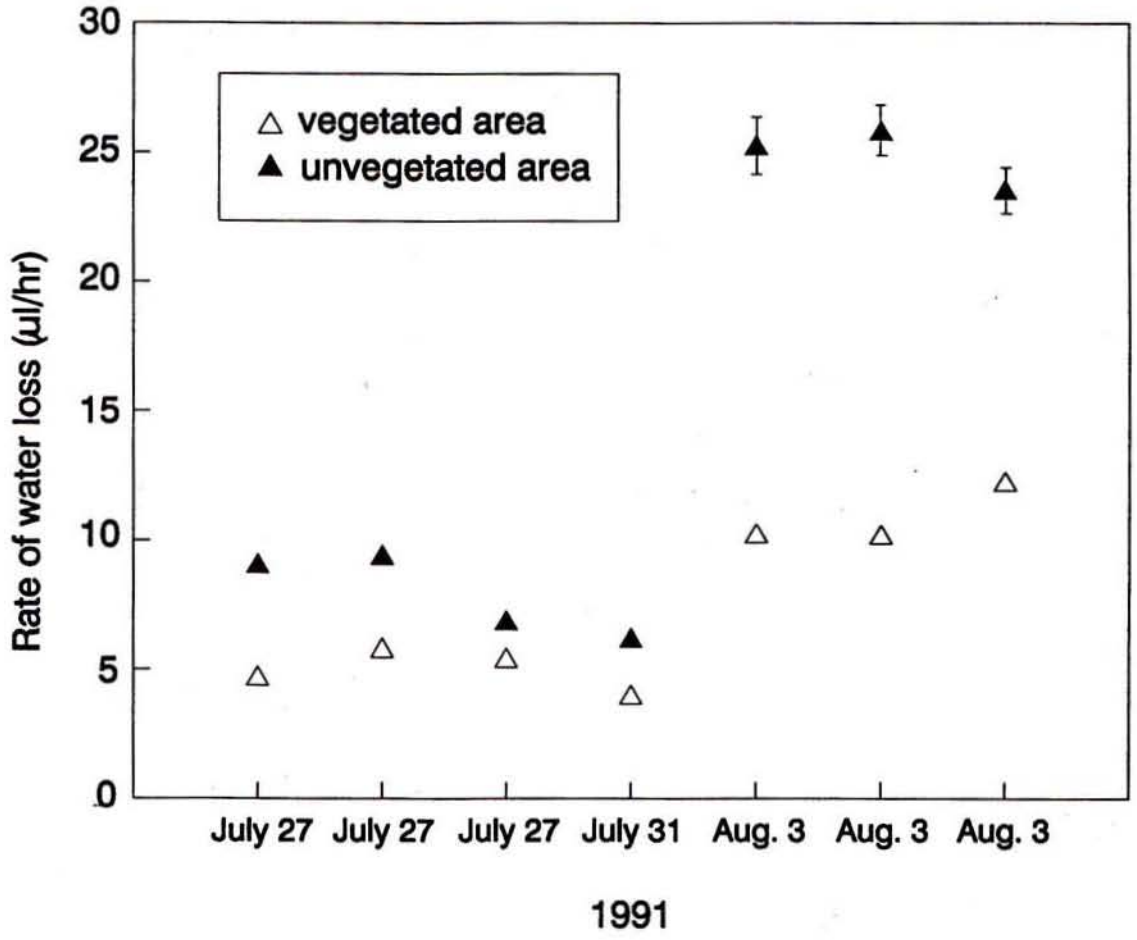


Table 4.3 Air temperatures on dates (in 1992) when evaporation occurred from tubes. Note that temperature data are for the whole day, but tubes were often in the soil for only part of the day. Time is in Central Daylight Saving Time.

Date tubes placed in soil	Dates tubes in soil	Maximum temp. (°C)	Minimum temp. (°C)	Average maximum temp. (°C)	Average minimum temp. (°C)
July 27	July 27 (1200h)	12.2	-0.3	15.7	2.7
	July 28	18.2	-0.2		
	July 29 (up to 1200h)	16.8	8.0		
July 31	July 31 (1200h)	12.4	1.9	13.9	2.8
	August 1	9.5	2.7		
	August 2 (up to 1200h)	19.9	3.7		
Aug. 3	August 3 (1200h)	26.0	7.8	26.8	10.2
	August 4 (up to 1200h)	27.6	12.5		

4.5 **Discussion**

In both 1991 and 1992, soils became more saline from early spring to mid-July. This increase in salinity (sodium concentration) coincided with a decrease in the water content of soils, and an increase in redox potential. By late August, 1991, soils had returned to salinity, moisture, and oxidation levels similar to those of early spring. Soil salinity, water content, and redox potentials therefore appear to be coupled in time. Similar seasonal trends in water content have been noted by Wilson (1993) in a more seaward portion of a La Pérouse Bay salt marsh. Seasonal trends in these soil variables are presumably caused by seasonal changes in air temperature (Fig. 1.4). High mid-summer temperatures increase evaporation rates from soil surfaces, as shown by the low water content of soils, and increase soil-water salinity both by concentrating soil water and by vertical advection as described later. The drier soils would also be more oxidized. Soil profiles support the importance of evaporation in mid-summer: salinity decreases with depth in the upper 6 cm. By contrast, salinity decreased between June and August, 1977, in a James Bay salt marsh (Glooschenko and Clark, 1982), perhaps reflecting the unusually high precipitation of 1977.

The salinity (sodium concentration) of soil water in the summer was inversely related to biomass: bare areas were more saline than low biomass areas, which in turn were more saline than high biomass areas. Biomass was a much better predictor of sodium concentration than water content, redox potential, or bulk density. When significant differences existed in salinity between biomass categories, soils of bare areas tended to be drier and more oxidized than those of high biomass areas, although differences were only significant in redox potentials obtained in 1992. Similarly low correlations between soil salinity and redox potential are reported by Howes et al. (1986) for a New England salt marsh. In an intertidal region of La Pérouse Bay, Wilson (1993) found bare areas to be not only drier than vegetated areas, as in this study, but also more reduced, contrary to the results of this study; differences may reflect the effects of tides, as her sites were more seaward than those used in this study. In the early spring of both 1991 and 1992, little difference in soil salinity existed between biomass categories. This is a result of flooding by meltwater (salinity c. 0.05 g

dissolved salts/l). The flushing and dilution of surface salts by meltwater is reflected in early spring soil profiles, which show an increase of salinity with depth to 10 cm. In the early spring, in fact, bare sites tended to be wetter and more reduced than high biomass sites. High biomass areas tend to have a thicker organic layer than bare sites, and are often slightly more elevated than surrounding areas because of the effects of past goose grubbing and erosion around intact swards. In the early spring, therefore, high biomass areas may be drained earlier than bare areas. Despite this tendency of bare areas to be wetter in spring, they quickly become drier and more saline than high biomass areas for most of the summer.

It is proposed that the inverse relationship between biomass and the salinity of soil water is caused by differences in water loss through evaporation. As described earlier, vegetation can reduce wind speeds, decrease soil temperature, or reduce surface permeability, all of which will reduce evaporation. This prediction is confirmed by the measurements of evaporation rates. Notably, differences in evaporation rates between vegetated and unvegetated areas increased with temperature. Differences between biomass categories in evaporative rate are therefore likely to increase from spring to mid-summer. Indeed, the largest differences between biomass categories in soil water salinity were observed in mid-summer. After August, salinity of soils is low and almost equal between biomass categories because a) soil water loss by evaporation at low fall temperatures is exceeded by water gain from precipitation, and b) high fall tides of low salinity (Jefferies et al., 1979, Price et al., 1989) may dilute and flush salts from the surface soil.

A high evaporation rate can increase the salinity of soil water either by reducing the amount of soil water, or by increasing the absolute amount of dissolved salts. Reduction of soil water cannot be the sole cause of high salinities in unvegetated areas, or else large significant differences between biomass categories would exist in water content as well as salinity. Furthermore, if the absolute amount of dissolved salts was constant, salinity increase would be inversely proportional to water content decrease. In fact, between June 16 and July 30, 1992, sodium concentration in the soil water increased 3-, 6-, and 7-fold in high biomass, low biomass and bare areas respectively, but volumetric water content only

decreased 1.6- to 1.7-fold over the same period. Similarly, in a New England salt marsh there was no difference in soil water content or redox potential, although soil-water salinity was higher in bare areas compared with vegetated areas (Bertness, 1991). In the inland, peaty regions of La Pérouse Bay, differences existed between bare and vegetated areas in soil-water salinity and in volumetric but not gravimetric water content (Iacobelli and Jefferies, 1991).

This suggests that evaporation increases the absolute amount of dissolved salts in soil water. Such an increase could occur either by advection (vertical or horizontal) or by molecular diffusion. In a James Bay salt marsh, horizontal advection predominated where the slope exceeded c. 3.3 m/km, but diffusion and vertical advection predominated in flatter terrain (Price and Woo, 1988b). The topography of the La Pérouse Bay salt marshes is relatively flat (slope c. 1.2 m/km), and there is little difference in elevation between vegetated and unvegetated areas (Chapter 3), so horizontal advection is thought to be of minor importance in explaining biomass-salinity relationships.

The increase in salinity with soil depth after the top 6 cm in several profiles (Fig. 4.2) suggests an upward movement of salts from deep deposits, and is consistent with an origin of salt marsh salts from buried Tyrell Sea sediments (Price and Woo, 1988 a,b; Price et al., 1989). A high evaporation rate, by decreasing the water potential at the soil surface, can increase the upward movement of saline soil water over short distances (against the gravitational potential). The pure water removed by evaporation is (partially) replaced by saline water, so the salinity of the surface soil water increases. Since the pure water removed by evaporation is partially replaced by deeper soil water, changes in the water content of the surface soil are small. The net effect is that differences in evaporation between biomass categories can lead to large differences in soil-water salinities, but only small differences in soil water content. This is consistent with the experimental results. Upward movement of salts can also occur by molecular diffusion but this is much slower than vertical advection (Nye and Tinker, 1977).

It is possible that the patterns in salinity reflect underlying patchiness in the salinity of Tyrell Sea sediments. If this difference in surface salinity affects plant growth (as shown in Chapters 5 and 6), differences in biomass and hence evaporation rate would be anticipated only as a consequence, not a cause, of salinity differences. According to this hypothesis, differences between areas in salinity and hence biomass would be constant through time. It is known, however, that many of the bare hypersaline areas were vegetated (and so presumably not very saline) a decade ago (Chapter 1). Other experiments have shown that the soil water salinity of an area can be decreased by increasing biomass (by exclosing areas from grazing; Chapter 5 and Bazely, 1984). Vegetation patterns are therefore a cause of soil-water salinity patterns, not just a consequence. Lastly, it is unlikely that uniformly laid down marine sediments had the chemical heterogeneity to cause the complex patterns in vegetation and surface salinity visible today.

Vegetated areas have an additional source of water loss: transpiration. Transpiration should decrease the water potential of the surface soil, decrease soil water content, and result in the preferential removal of pure water (by the partial exclusion of salt by roots). All these effects are predicted to make vegetated areas saltier than unvegetated areas, when in fact the reverse trend is found. Water loss per unit area by direct evaporation from sediments must therefore exceed transpirational loss per unit area of sward in this system.

In summary, differences between biomass categories in soil-water salinity are caused by differences in evaporation, which affects the upward flow of water from fossil salt deposits. The importance of evaporation is further illustrated by the large seasonal trends in soil water salinity.

Reduction of evapotranspiration by vegetation has been reported in several other studies. In a sedge-dominated coastal fen in James Bay, evapotranspiration (relative to evaporation from open water) decreased as a site became vegetated (Lafleur, 1990). Evapotranspiration in temperate wetlands is reported to be reduced relative to that from open water (Linacre, 1970), although this effect may vary with vegetation type (Ingram, 1983).

Evapotranspiration is also reported to decrease as the planting density of crops increases (McCauley et al., 1978). Decreased evaporation has been recorded in the immediate vicinity of hedgerows and similar agricultural windbreaks because of reduced wind speeds (Lomas and Schlesinger, 1971; McNaughton, 1983). Higher and more variable soil temperatures have been reported in bare soil compared to vegetated soil, leading to increased evapotranspiration (Monteith and Szeicz, 1961; Iacobelli and Jefferies, 1991). By contrast, measurements of evapotranspiration under and away from shrubs in desert ecosystems have not shown any effect of vegetation (Evans et al., 1981), perhaps reflecting the low density of vegetation in such ecosystems.

An inverse relationship between soil-water salinity and biomass has been reported earlier for temperate salt marshes (Adams, 1963; Hanson, 1982, in Bakker, 1985; Joenje, 1985; Bertness, 1991), for arcs of vegetation in a saline area of desert in Jordan (White, 1969) and for the more inland, peaty regions of La Pérouse Bay (Iacobelli and Jefferies, 1991). Dieback of salt marsh vegetation, through wrack deposition or shading, is reported to cause the formation of hypersaline salt pans (Pethick, 1974; Boston, 1983). In all cases, increased evaporation from bare areas was suggested as the cause of these differences in soil salinity.

In this study, soil-water salinity increased with the size of the bare patch, similar to the results of Bertness (1991). If plant growth and invasion of bare patches is limited by salinity (Chapter 5), then the larger a bare patch is, the more likely it will remain unvegetated and indeed grow in area. There may therefore be a threshold in size beyond which bare areas do not convert back to vegetated areas. Conversely, once vegetation begins to encroach upon a bare area and so reduce the patch size, edaphic conditions may ameliorate, allowing further revegetation. This potential for facilitation in salt-marsh vegetation has been discussed by Redfield (1972) and Bertness (1991).

CHAPTER 5: EFFECT OF SOIL SALINITY AND INTRASPECIFIC COMPETITION ON GRAMINOID GROWTH IN A SALT MARSH

5.1 Introduction

Halophyte growth in salt marshes is affected by a combination of abiotic and biotic factors (Adam, 1990). Zonation of coastal salt marsh vegetation may reflect different tolerances of species to physical conditions, including soil salinity, on the seaward limits of species distribution, and different interspecific competitive abilities on their landward limits (Bertness and Ellison, 1987; Ungar, 1991). Transplant and removal studies in New England, Alaska and New Zealand salt marshes have found that species from more seaward marsh vegetation grow well in less saline and more landward marsh zones when interspecific competition is reduced, but not with "normal" levels of interspecific competition (Silander and Antonovics, 1982; Snow and Vince, 1984; Bertness and Ellison, 1987; Partridge and Wilson, 1988; Bertness, 1991a,b). Similary, species of the most saline zone of an Ohio salt pan grow best in less saline areas only when interspecific competition is reduced (Ungar et al., 1979; Ungar, 1991). More landward marsh species, by contrast, grow poorly under the harsh physical conditions of more seaward marsh zones, irrespective of the occurrence of competition (Snow and Vince, 1984; Bertness and Ellison, 1987; Partridge and Wilson, 1988; Bertness 1991a,b).

Intraspecific competition is reported to be relatively unimportant in causing mortality in *Salicornia* spp. (Jensen and Jefferies, 1984; Ungar, 1991; Ungar, 1987; Ellison, 1987a) although intraspecific competition can reduce plant size (Ungar, 1987; Ellison, 1987a). The effects of physical factors, such as high salinity and flooding, are suggested to be more important than intraspecific competition in affecting demographic patterns in *Salicornia* populations (Jensen and Jefferies, 1984; Ellison, 1987b; Ungar, 1991). In *Atriplex triangularis*, however, density-dependent mortality has been reported (Drake and Ungar, 1989; Ellison, 1989). Differences in density-dependent mortality between these two species have been attributed to differences in plant geometry, with the greater branching and plant

height of *Atriplex triangularis* being responsible for its density-dependent mortality (Ellison, 1987a, 1989). Interactions between intraspecific competition and salinity tolerance are particularly evident in the demography of *Hordeum jubatum* plants in an inland saline marsh (Badger and Ungar, 1991). In years with high precipitation and hence low soil salinities, seedling survival was lowest in the zone with most intraspecific competition, not the most saline zone. Soil salinities increased in all zones in an unusually dry year, and seedling survival was then lowest in the most saline zone, not the zone with most intraspecific competition.

This study examines the role of both salinity and intraspecific competition on the demography of *Puccinellia phryganodes* in the salt marsh at La Pérouse Bay, Manitoba. Limited results for *Carex subspathacea* are also presented. Specifically, graminoid growth is examined in sites of differing plant density. Previous results (Chapter 4) indicate that soil salinity is inversely related to plant density in this salt marsh. Growth of plants in areas of low plant density may therefore be restricted by high soil salinities but enhanced by low intraspecific competition. If the negative effects of salinity outweigh the positive effects of low intraspecific competition, plant growth will be poor in areas of low plant density, and the plant density of such areas may decrease further.

Since *Puccinellia* is more salt-tolerant than *Carex* (Chapters 1, 6), and assuming equal effects of intraspecific competition on the growth of both species, the growth of *Puccinellia* is expected be less affected by differences in graminoid density than that of *Carex*.

Previous studies have found grazing (Bazely and Jefferies, 1989) and plant origin (Sadul, 1987) to be important determinants of the growth of plants of *Puccinellia phryganodes*. The effects of grazing and origin on the demography of *Puccinellia* plants are therefore also examined, by the use of exclosures and reciprocal transplants respectively.

Lastly, the effects of algal crusts on *Puccinellia* growth are examined. Algal crusts occur only in areas with little or no vegetation, so negative effects of algal crusts on growth

may augment soil salinity in decreasing growth in areas of low plant density.

5.2 **Hypotheses**

1) Graminoid growth (including survivorship) is inversely related to sward density or biomass.
2) Graminoid growth (including survivorship) is reduced by soil salinity (positive feedback hypothesis 2; Chapter 1).
3) Graminoid growth (including survivorship) is reduced by intraspecific competition.
4) Grazing affects *Puccinellia phryganodes* growth and survivorship.
5) *Puccinellia phryganodes* plants originating from swards of different densities have different growth patterns.
6) *Puccinellia* growth is less affected by differences in plant density than is *Carex* growth.
7) Algal crusts reduce graminoid growth (including survivorship).

5.3 **Methods**

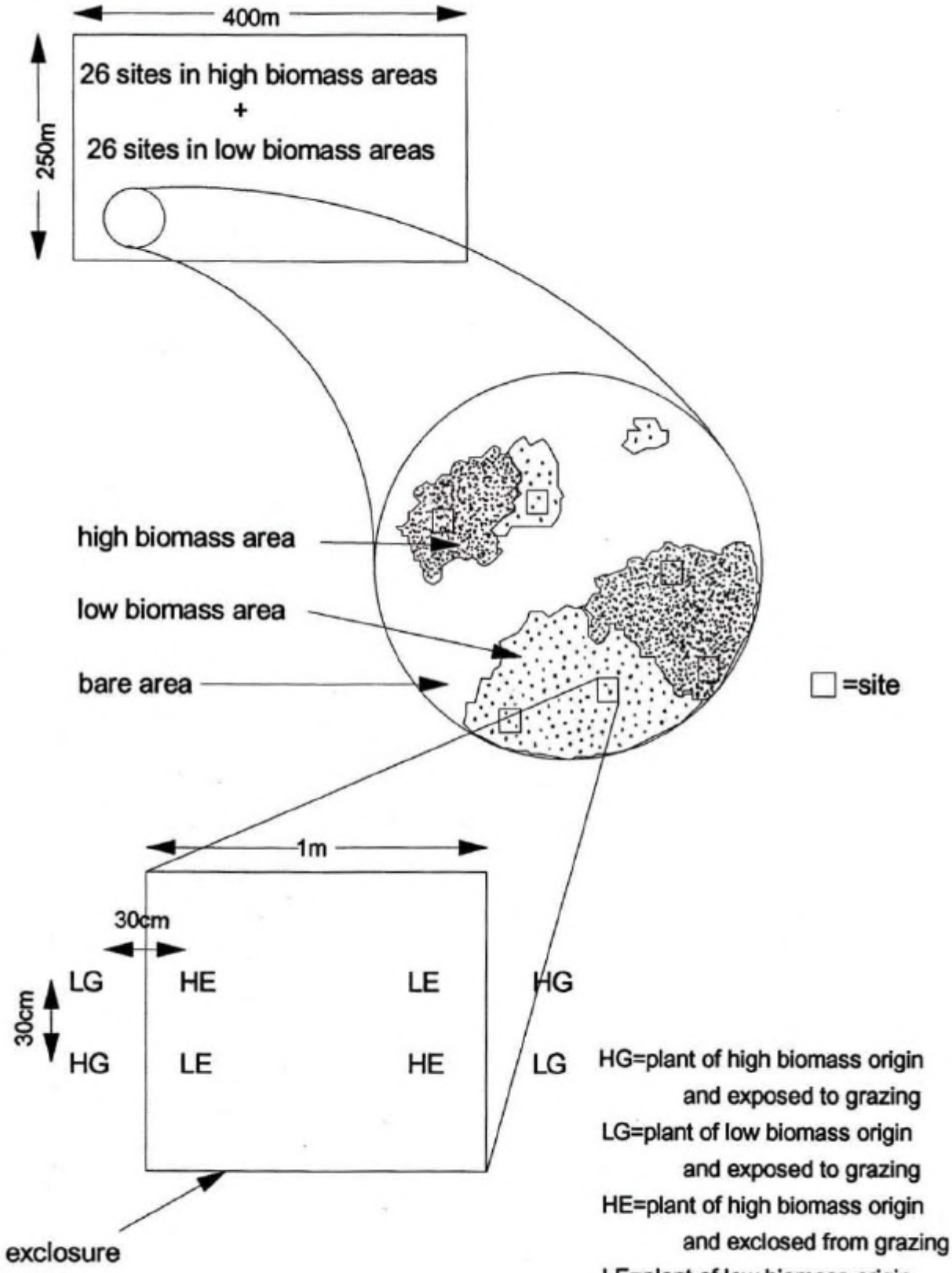
5.3.1 Methods for examining the demography of *Puccinellia* plants in high and low biomass areas (1991)

5.3.1.1 Field methods

In early June, 1991, 26 high biomass and 26 low biomass sites were selected in a c. 250 m x 400 m area of salt marsh on the eastern shore of La Pérouse Bay. This study area was not inundated by tides at any time during the study period, and includes all plots used for the analysis of seasonal trends in salinity (Chapter 4).

Each site contained two planting areas 1 m apart. In each planting area, two plants were transplanted from a high biomass sward, and two plants were transplanted from a low biomass sward. One plant from each sward type was exclosed from goose grazing by poultry netting (Fig. 5.1). Each site, therefore, had two plants representing each possible

Fig. 5.1. Experimental design to determine the effects of site biomass, grazing, and origin on the growth of *Puccinellia phryganodes* in 1991. The approximate dimensions of the study area, on the eastern salt marsh, are shown, as well as the positions and dimensions of sites within this study area. Note that there are two replicates for each grazing level x origin category in each site.


400m
250m
26 sites in high biomass areas
+
26 sites in low biomass areas
high biomass area
low biomass area
bare area
□=site
1m
30cm
30cm
LG
HE
LE
HG
HG
LE
HE
LG
exclosure
HG=plant of high biomass origin
and exposed to grazing
LG=plant of low biomass origin
and exposed to grazing
HE=plant of high biomass origin
and exclosed from grazing
LE=plant of low biomass origin
and exclosed from grazing

combination of origin (high biomass, low biomass) and grazing level (grazed, exclosed). Assignment of plants to patches were made at random (see below).

To assess the effect of plant origin, plants could have been selected from a single patch of high biomass sward and from a similar patch of low biomass sward. Since plants from a small patch are genetically similar (Sadul, 1987), variation in demographic parameters between plants of a similar origin is likely to be low, and demographic differences between plants with different origin or grazing level would be easily observed. In this design, however, any effect of origin ultimately reflects just the genetic differences between two patches. It is more desirable to assess genetic differences between plants originating from high biomass and low biomass swards in general. This can be acheived by selecting plants from a variety of high biomass and low biomass patches in the salt marsh, and then randomly assigning them to transplant sites.

A total of 50 high biomass and 50 low biomass patches were identified in the salt marsh; the 26 high biomass and 26 low biomass transplant sites were later randomly selected from these patches. Two 4 cm x 4 cm turves were collected from two predetermined areas in each site. Two *Puccinellia* plants were removed from each turf at random, giving a total of 200 plants of high biomass origin and 200 plants of low biomass origin. Each transplant site was then randomly assigned four plants of high biomass origin and four plants of low biomass origin.

After their removal from turves, plants were stored overnight in water-filled vials, and then transplanted the following day, June 6, 1991. Transplanted plants could be identified from other plants by orange- or yellow-painted toothpicks inserted on either side of the shoot; the colour of the toothpicks identified plant origin.

Plant growth was assessed using non-destructive demographic methods. The demography of plants was scored on the following five census dates: June 11-13, June 25-28, July 9-10, July 24-25, and August 7-9. Adverse weather conditions on June 26 and 27

accounted for the four day census period on June 25-28. Plants were examined in the same order on all census dates to minimize differences in interval lengths between individual plants. Detailed description of demographic techniques and analyses are given in Chapter 2. Both seasonal and interval-based demographic parameters were calculated. It should be noted that seasonal demographic paramters are calculated for even those plants that died during the experiment (otherwise data would be biased towards the healthiest plants). Mortality values are presented for comparison. Results for interval-based demographic parameters are less useful than seasonal demographic parameters in this situation (Chapter 2) and so are only presented in Appendix 2.

Originally, this transplant experiment was designed to allow a simple comparison between plant growth in high biomass and low biomass sites. By the last census date, however, it was obvious that considerable variation existed in the demography of plants in low biomass sites. It was also evident from measurements of salinity in nearby plots that the salinity of soil water was especially variable among low biomass areas. Spatial variation in salinity may account for variation in plant growth in low biomass sites. Alternatively, differences in plant density (biomass) in low biomass sites might explain variation in plant growth. On August 15, 1991, two turves of c. 8 cm x 8 cm x 4 cm deep were collected from each low biomass site (one from each planting area), and from 10 of the 25 high biomass sites. The exclosures were broken into by geese just prior to the final census date, and the exclosed biomass heavily grazed (this did not affect values of plant demographic parameters). Biomass was therefore measured only in the originally grazed areas. The top centimeter of soil was pooled from both turves, and soil water extracted by centrifugation as described earlier (Chapter 2). Graminoid density (shoots/cm^2), aboveground biomass (Chapter 2), and gravimetric water content (Chapter 4) were determined on one randomly selected turf for each site. The number of turves that could be analyzed was severely limited by time restrictions as the soils dry quickly and plant growth occurs. Therefore, duplicate measurements were not obtained for each site, and turves were not collected from all high biomass sites.

5.3.1.2 Statistical analysis

Almost all (8/10) of the high biomass sites had a sodium concentration between 0 and 2 g/l in extracted soil water. The soil water of the other 2 high biomass sites had a sodium concentration between 2 and 3 g/l. By contrast, the soil water of low biomass sites varied in sodium concentration from 1.33 to 18.1 g/l; this consisted of 10 sites with 0 to 2 g/l, 8 sites with 2 to 4 g/l, 7 sites with 4 to 8 g/l, and one site with 18.1 g/l. This range of data suggests four categories of seven sites each: high biomass (0 to 2 g/l Na^+), low biomass (0 to 2 g/l Na^+), low biomass (2 to 4 g/l Na^+), low biomass (4 to 8 g/l Na^+). Several of the sites had missing plants (largely through goose uprooting), and so were not suitable for statistical analysis. The remaining sites were reduced to seven sites/category by random selection.

The formal symbolic notation for the experimental design is $R_2(O_2xG_2xS_7(T_4))$: that is, seven sites (S) are nested in four treatments (T), and each site is crossed with two grazing levels (G) and two origins (0), with two replicates (R) for each combination of the previous variables. Fixed variables include T, G, and O, while S and R are random variables. A sample ANOVA table is given in full in Appendix 1.

The dependent variables for an ANOVA analysis (regression terminology is used here since ANOVA is a type of regression analysis) are the seasonal demographic variables: main shoot leaf birth rate (MSLB), main shoot leaf death rate (MSLD), axillary shoot leaf birth rate (ASLB), axillary shoot leaf death rate (ASLD), total leaf birth rate (TLB=MSLB+ASLB), total leaf death rate (TLD=MSLD+ASLD). Since there are multiple dependent and intercorrelated variables, a MANOVA is appropriate prior to individual ANOVAs. The ASLB, ASLD, and TLD data were log-transformed (log (x+0.001)) and the TLB data was square root transformed because of heteroscedasticity. All transformed data passed Bartlett's test of homogeneity or the F-max test (Kirk, 1982). Since many shoots had values of zero for ASLB or ASLD, the distributions of ASLB, ASLD, TLB, and TLD were negatively skewed and slightly leptokurtic despite transformations. Depatures from normality, however, do not seriously affect ANOVA results if all populations are homogeneous in form (Kirk, 1982; Day and Quinn, 1989).

All planned comparisons were based on the use of F tests. These included comparisons of the demography of plants in average high biomass and low biomass sites and the effect of increasing salinity on plant demography in low biomass sites. Although the comparison of plant demography in high and low biomass sites with a similar soil-water salinity is also of *a priori* interest, this planned comparison is not orthogonal to the previous two. Since the power of the previous two comparisons would be reduced considerably by statistical analysis of this comparison, it is not analyzed statistically. In any case, regression analyses (see below) examine the importance of density *per se*. Although the data have been truncated slightly, the average salinity of the soil from each biomass category was essentially unaffected by this procedure. For example, approximately a third of low biomass sites fell into each of the three treatment categories. Comparisons between averages in the set of truncated data are therefore representative of comparisons of averages of the original data.

After the above ANOVA analyses, regression analyses were carried out, both on the full data set, and on just the low biomass sites. Interaction terms sometimes appear significant in regression analyses only because they are strongly correlated with one of their component variables. To prevent such spurious results, interactions between variables were "pure" (ie., interaction terms were completely uncorrelated with their components, including lower order interactions). Specifically, residuals from the regression of components on the original interaction term were used in place of the original interaction term. This is a common technique in regression analysis (D. Burrill, Statistical Consulting Service, OISE, pers. comm.).

All statistical analysis used SAS software (SAS, 1988).

5.3.2. Methods for examining the demography of *Puccinellia* plants in high biomass, low biomass and bare areas (1992)

5.3.2.1 Field methods

Based on the results of 1991, it was desirable to examine plant growth in sites

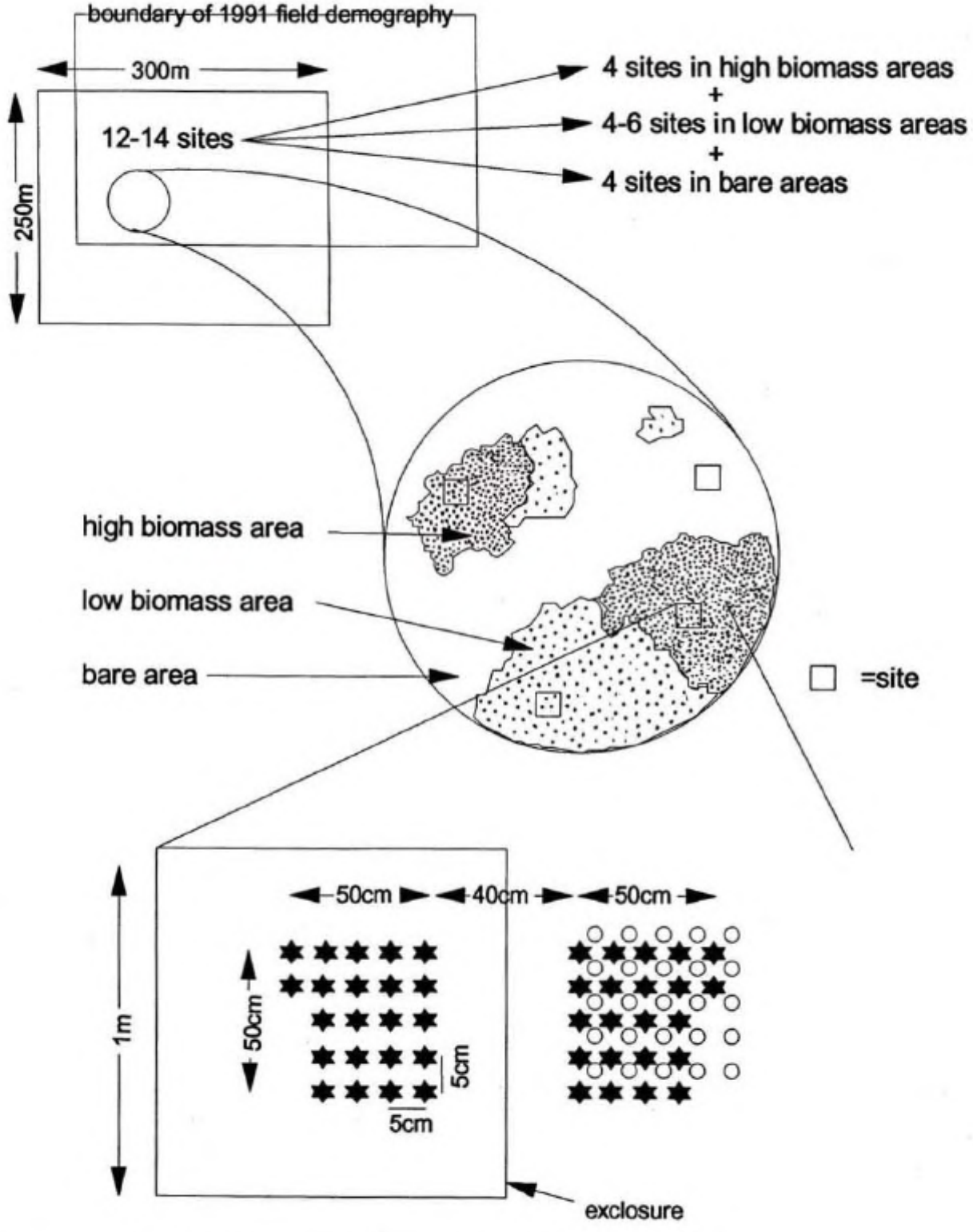
representing a wider spectrum of biomass (ie, bare sites as well as high biomass and low biomass sites), and to examine biomass, soil salinity, and other soil variables at sites throughout the season rather than just at the end of the season. The effect of grazing was also examined, for comparison with results obtained in 1991. The response of the other major graminoid, *Carex subspathacea*, to gradients in site biomass was also of interest (see section 5.1).

Since plant origin was found to be have a minor contribution to variance in 1991, all plants had the same origin, a 1 m^2 area of *Puccinellia-Carex* high biomass sward.

The experimental design was as follows (Fig. 5.2). Each of three biomass categories (high biomass, low biomass, bare sediment) was represented by four sites. Each site contained 22 *Puccinellia* plants transplanted in each of two adjacent 50 cm x 50 cm areas; one area was exclosed by poultry netting. The centers of the adjacent areas were at most 70 cm apart, so all plants within a site presumably experienced similar edaphic conditions. Unlike the design in 1991 which had a few plants at many sites, this design has many plants at a few sites. It would not have been possible to analyze the salinity and biomass of many sites throughout the season; in addition, many plants per site give a better characterization of growing conditions at a site.

The sites for each biomass category were selected to represent the average soil salinity of that biomass category. Since soil-water salinity is uniform between sites in the early spring, plants were transplanted into six sites per biomass category. Four sites per biomass category were selected from these six sites on July 12, when salinity differences between biomass categories were evident. Specifically, soil-water salinity of the six transplant sites/category was compared to that of an independent set of 14 plots/category (described earlier in Chapter 4). For each site, soil water was extracted by centrifugation, as described earlier (Chapter 2), from the top 1 cm of a c. 10 cm x 10 cm block of soil, and the salinity of the soil water was analyzed by a salinity/conductivity meter (Yellow Springs Instrument Co. Inc., Ohio, U.S.A., model 33) after dilution. The mean salinity of the demography sites

Fig. 5.2. Experimental design to determine the effects of site biomass and grazing on the growth of *Puccinellia phryganodes* and the effect of site biomass on the growth of *Carex subspathacea* in 1992. The approximate dimensions of the study area, on the eastern salt marsh, are shown and compared to that in 1991, as well as the positions and dimensions of sites within this study area. Note that there are 22 replicates of *Puccinellia* for each grazing level category (grazed, exclosed) in each site. In high biomass and bare sites, but not low biomass sites, there are 25 replicates of *Carex* in the grazed area of each site.



★= Puccinellia plant (transplanted into all sites)

○=Carex plant (transplanted into high biomass and bare sites)

chosen to represent each biomass category approximates to the mean salinity of the soils from the 14 plots/biomass category (Table 5.1). As in 1991, low biomass sites had greater variability in soil salinity than high biomass sites. Although only four sites/category were used in the ANOVA analysis, all six low biomass sites were followed throughout the season which allowed regression analyses to be carried out on the data.

In addition, 25 *Carex* plants were transplanted into the grazed area of the high biomass and bare sites, interspersed among the previously described *Puccinellia* plants. If the growth of *Carex* is more sensitive to salinity than that of *Puccinellia*, then its growth will be more reduced between high biomass and bare sites than that of *Puccinellia*.

Plants were transplanted on June 20-22, 1992. Plant demography was examined on three census dates about 17 days apart: June 30-July 2, July 16-19, and August 3-4. Sites were examined in the same (randomized) order on each date to reduce differences in the between-census intervals. Demographic techniques are described in full in Chapter 2. Only seasonal demographic parameters could be calculated for all sites. Since there were only two intervals, interval-based leaf birth and death rates could only be calculated for some plants (presented in Appendix 2), while leaf lifespan calculations are not valid (ie., there is only one possible value for leaf lifespan). The late season of 1992 prevented more census dates. Most plants did not produce axillary shoots. Therefore, the seasonal demographic parameters ASLB and ASLD were not calculated. TLB and TLD were calculated, and are similar in value to MSLB and MSLD, respectively. The sample size was randomly reduced to 18 plants/plot since a few plants were removed by geese.

A block of soil (c. 8 cm x 8 cm x 4 cm deep) was removed from each of the exclosed and grazed areas of all sites on June 26, July 12, July 21, and July 30. Care was taken not to disturb or affect transplanted plants by soil removal. From each soil block, above-ground biomass ($g_{dry\ wt}/m^2$), sodium concentration of extracted soil-water (g/l), gravimetric water content ($g_{water}/g_{dry\ soil}$), bulk density ($g_{dry\ soil}/cm^3$), and redox potential (Eh values) were determined as described in Chapter 4. Areas were exclosed from June 26, the first date of

Table 5.1. Salinity (g dissolved salts/l) in grazed and exclosed areas of demography plots (numbered) in high biomass (H), low biomass (L) and bare (B) sites. Plots were compared to average ($\pm$ SD) salinity of 14 other plots in grazed areas, and two plots from each biomass category were rejected on the basis of having higher or lower salinity than this average. The high salinity of the grazed area of H4 was assumed to be a measurement error, and indeed sodium concentrations of H4 (grazed) were later found to be less than that of H6 (grazed) on July 12, July 21, and July 30.

Site	Grazed areas	Exclosed areas	Average of grazed and exclosed areas	Reason for rejection
H1	10.0	7.2	8.6	
H2	6.6	6.1	6.4	
H3	8.1	6.1	7.1	
H4	20.2	9.6	14.9	
H5	7.7	4.9	6.3	salinity too low
H6	17.2	23.1	20.2	salinity too high
14 high biomass sites	12.2 (± 5.5)			
L1	48.8	28.1	38.5	
L2	42.1	45.5	43.8	
L3	22.1	36.8	29.5	
L4	38.0	11.8	24.9	
L5	11.9	12.8	12.4	salinity too low
L6	12.8	12.4	12.6	salinity too high
14 low biomass sites	29.0 (± 15.9)			
B1	39.2	26.0	32.6	
B2	50.9	45.2	48.0	
B3	31.4	48.7	40.0	
B4	35.0	31.0	33.0	
B5	53.3	44.2	48.8	salinity too high
B6	56.7	46.7	51.7	salinity too high
14 bare sites	35.9 (± 14.8)			

soil sampling, so this date represents pre-exclosure conditions.

5.3.2.2 Statistical analysis

The experiment was designed to be analyzed by a three-way ANOVA, with four sites nested in each of three biomass categories, all crossed by two grazing treatments (grazed, exclosed). The seasonal demographic data (TLB and TLD), however, was not normally distributed and had unequal variances, even after numerous transformations. This was largely due to extensive mortality in low biomass and bare sites. On many plants no new leaves were born, and all the original (2 to 3) leaves died, both of which lead to low TLB and TLD variances. Data were therefore analyzed by the non-parametric Friedman's test (version for replicated designs, Chi-squared statistic; Gibbons, 1985). Since Friedman's test is appropriate only for two-way designs, sites of all three biomass categories were examined together in a site ($k=12$) by grazing treatment design. Both site and grazing treatment effects can be examined by switching which variable is considered the block effect (Miller, 1966). Once a significant site effect was established, the effect of biomass category could be examined by a planned comparison between sites of each biomass category; the Wilcoxon Rank Sum test (Sokal and Rohlf, 1981) was used, because of the non-parametric nature of the data. Although interaction cannot be explicitly tested in this design, the effect of grazing and site within each biomass category was examined by individual Friedman tests.

Again, in the regression analysis, the interaction terms were uncorrelated with components, leaving a "pure" interaction term.

5.3.3 Methods for examining the demography of *Puccinellia* in bare areas with and without algal crusts (1992)

Three sites were selected with a uniform, thick, blistering and dry algal crust on the sediment surface. Sites were approximately 100 m apart. At each site, a 1 m x 2 m area was exclosed from goose grazing. Minimal and highly patchy grazing occurs at the planting density described shortly, and so exposure to geese would have increased data variance with

little gain in information. In each exclosed area, the algal crust was carefully removed with a scalpel from 25 circles of 10 cm diameter. The distance between the centers of adjacent circles was at least 22 cm.

A total of 150 individual *Puccinellia phryganodes* plants of similar size were isolated from a 15 cm x 20 cm turf. Genetic variability among plants from the same small area is predicted to be low (Sadul, 1987). On July 6, 1992, one *Puccinellia* plant was transplanted into the center of each circle from which crust was removed, and a total of 25 plants per exclosure were planted in intact algal crust at least 15 cm from the center of nearby circles (n=25 plants/treatment/site).

Growth of the transplanted *Puccinellia* plants was measured using demographic techniques described earlier (Chapter 2). Census dates were 13 days apart, on July 7, July 20, and August 2, 1992. Only the seasonal demographic parameters of total leaf birth (TLB) and total leaf death rate (TLD) were calculated. Interval-based demographic analyses are not suitable for this experiment because only two intervals exist (Chapter 2). Since virtually no plants produced axillary shoots, TLB and TLD are essentially synonymous with, respectively, MSLB (main shoot leaf birth rate) and MSLD (main shoot leaf death rate). Non-parametric statistical analyses were used for leaf birth and death rate data since these data were both non-normally distributed (Shapiro-Wilks, $p < 0.01$) and had heterogeneous variances (Bartlett's, $p < 0.05$) even with standard transformations.

Algal crust was removed in an additional three circles of 5 cm diameter for soil sampling. On July 27, 7 cm x 7 cm x 4 cm deep blocks of soil were collected from each circle, and under intact algal crust in three places per exclosure. Range of redox potentials from just subsurface to 2 cm depth was determined for each soil sample (Pt electrode). Soil bulk density and gravimetric water content were determined for the top 1 cm of each sample. Soil-water was extracted by centrifugation from the top 1 cm of each sample, and assayed for sodium as described earlier (Chapter 2).

5.4 Summary of results

1. Biomass and soil salinity differed between sites from different biomass categories, and between grazed and exclosed high biomass sites. Soil salinity was inversely related to plant density or biomass in sites in 1991 and 1992. In sites where exclosure increased biomass, soil salinity was also reduced.

2. Plant mortality and axillary shoot production differed between biomass categories and between years. In both years, mortality and axillary shoot production was inversely related to biomass. In 1992, mortality was greater and axillary shoot production was less than in 1991.

3. Leaf demography did not differ between plants in high and low biomass sites in 1991, but did differ in 1992 between plants in high and low biomass sites, and between plants in low biomass and bare sites. In 1992, total leaf birth and death rates were highest for plants in high biomass areas and lowest for plants in bare areas.

4. Grazing and plant origin had complex effects on leaf demography in 1991, and grazing increased leaf deaths in 1992.

5. Within the low biomass sites, leaf demography was a function of both salinity and plant density in 1991.

6. Within sites of similar soil salinity, leaf demography of axillary shoots was a function of plant density.

7. Regression analyses involving sites from all biomass categories indicated that both salinity and density were important determinants of leaf demography in both 1991 and 1992.

8. *Carex* growth was also greater in high biomass areas than in bare areas.

9. Algal crusts reduced *Puccinellia* growth in bare areas.

5.5 **Details of results**

5.5.1 Biomass and soil salinity differed between sites from different biomass categories, and between grazed and exclosed high biomass sites.

5.5.1.1 1991

In 1991, the 28 study sites varied both in plant density and soil-water salinity (Fig. 5.3). The average (± SE) plant density in high biomass sites was 4.64 (± 0.53) plants/cm^2, and in low biomass sites was 0.83 (± 0.08) plants/cm^2. This corresponded to an average biomass (grazed areas) of 27.17 (± 3.28) $g_{dry\ wt}/m^2$ in high biomass sites, and 17.20 (± 1.52) $g_{dry\ wt}/m^2$ in low biomass sites. The sodium concentration in extracted soil water varied from 0.66 to 7.36 g/l, as described earlier, with an average of 1.11 (± 0.16) g/l in high biomass sites, and 3.43 (± 0.48) g/l in low biomass sites. High biomass and low biomass sites had similar gravimetric water content (1.18 ± 0.09 $g_{water}/g_{dry\ soil}$ vs. 1.26 ± 0.07 $g_{water}/g_{dry\ soil}$, respectively).

5.5.1.2 1992

On June 26, immediately after exclosure of areas, grazed and exclosed areas within a site had similar above-ground biomass and similar sodium concentrations in the soil water (Fig 5.4.a-d). By and after July 12, exclosed areas had more biomass than grazed areas in all high biomass sites. Specifically, on July 21 and July 30 exclosed areas of high biomass sites had an average of 40 $g_{dry\ wt.}/m^2$ more biomass than grazed areas. In low biomass sites, however, there was no consistent difference in biomass between grazed and exclosed areas. Bare areas were devoid of vegetation with and without exclosure. Both grazed and exclosed areas of high biomass sites increased in above-ground biomass between June 26 and July 30, but low biomass sites generally showed little change in biomass over time. Low biomass sites 5 and 6, excluded from the ANOVA analyses because of below average soil salinity, showed an increase in biomass over the study period, with the biomass of site 6 approaching that of

Fig. 5.3 Sodium concentration in soil water as a function of shoot density of sites in 1991. Sites were divided into four treatment categories for analysis: * = high biomass (0 to 2 g/l Na^+), ▵ = low biomass (0 to 2 g/l Na^+), ○ = low biomass (2 to 4 g/l Na^+) and ▫ = low biomass (4 to 8 g/l Na^+).

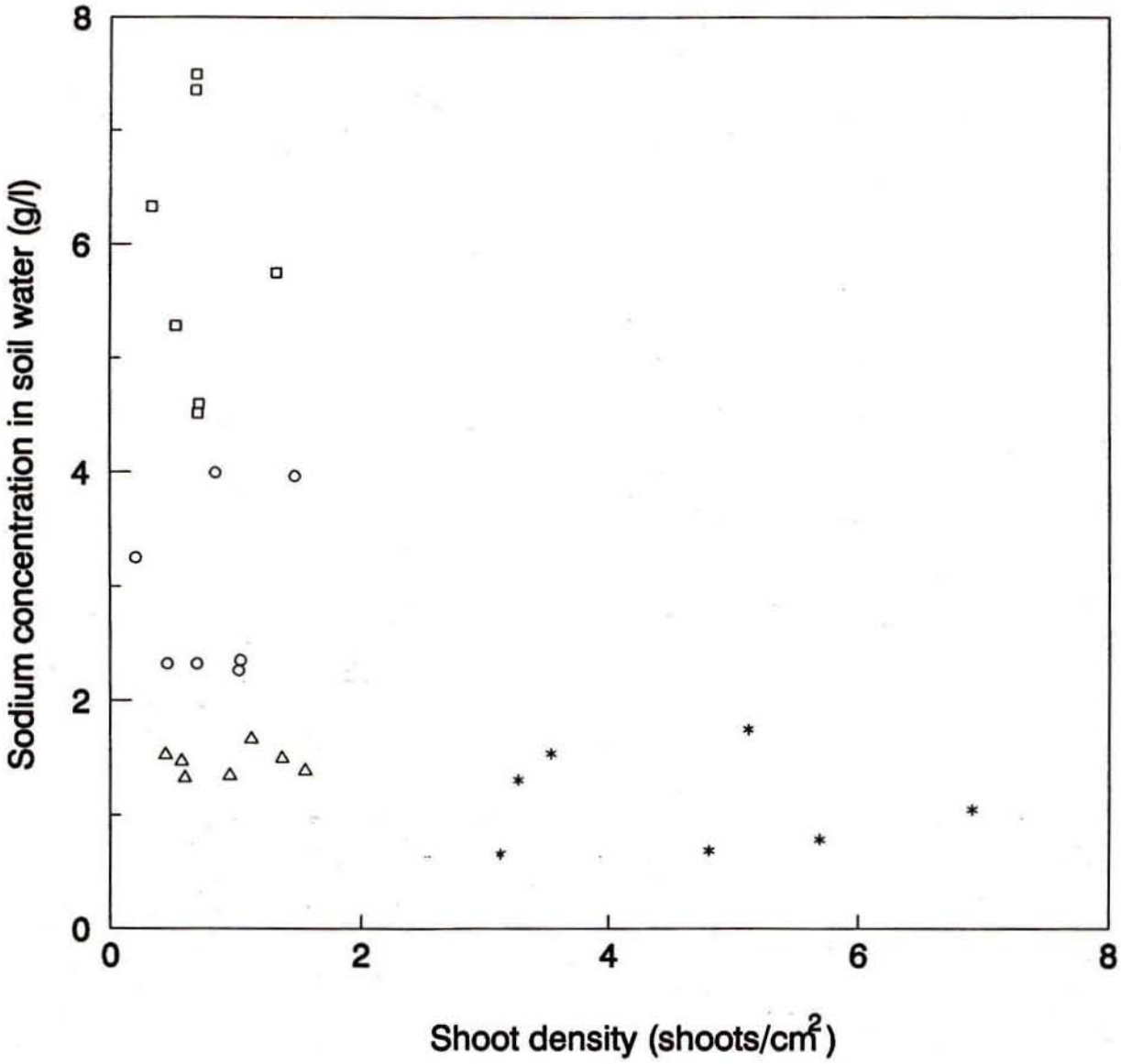
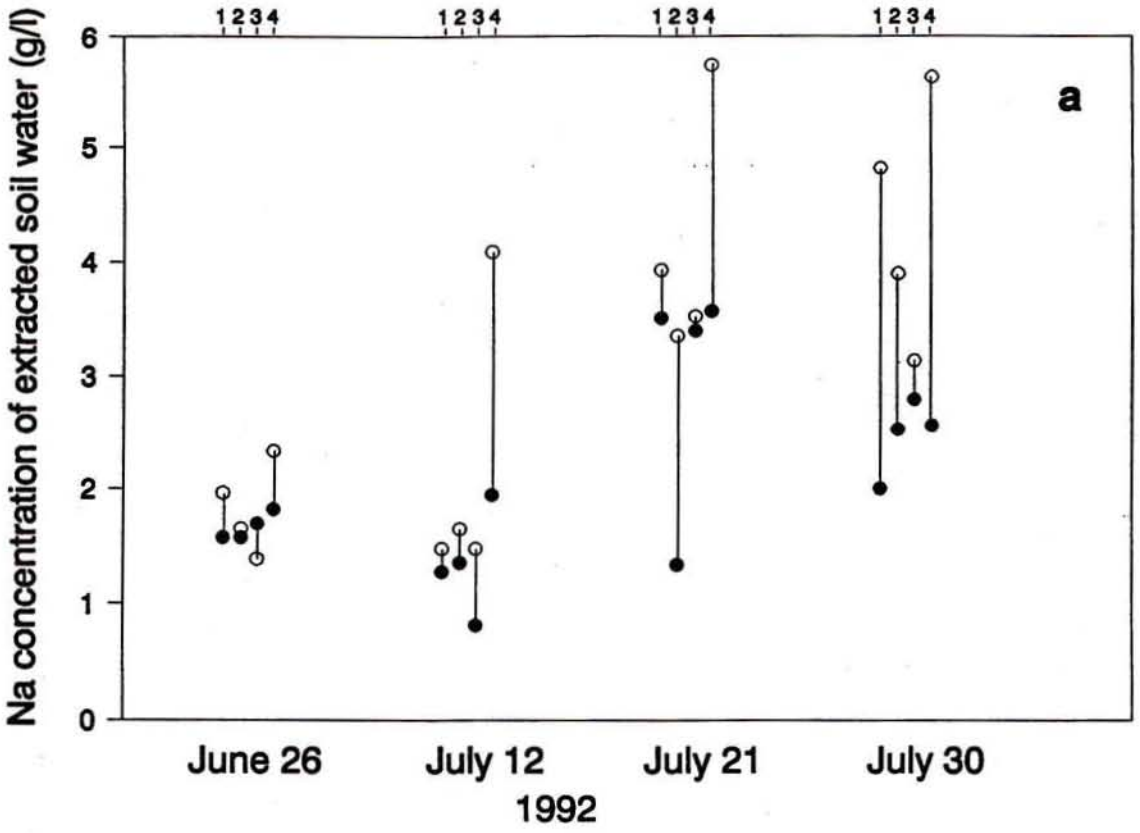
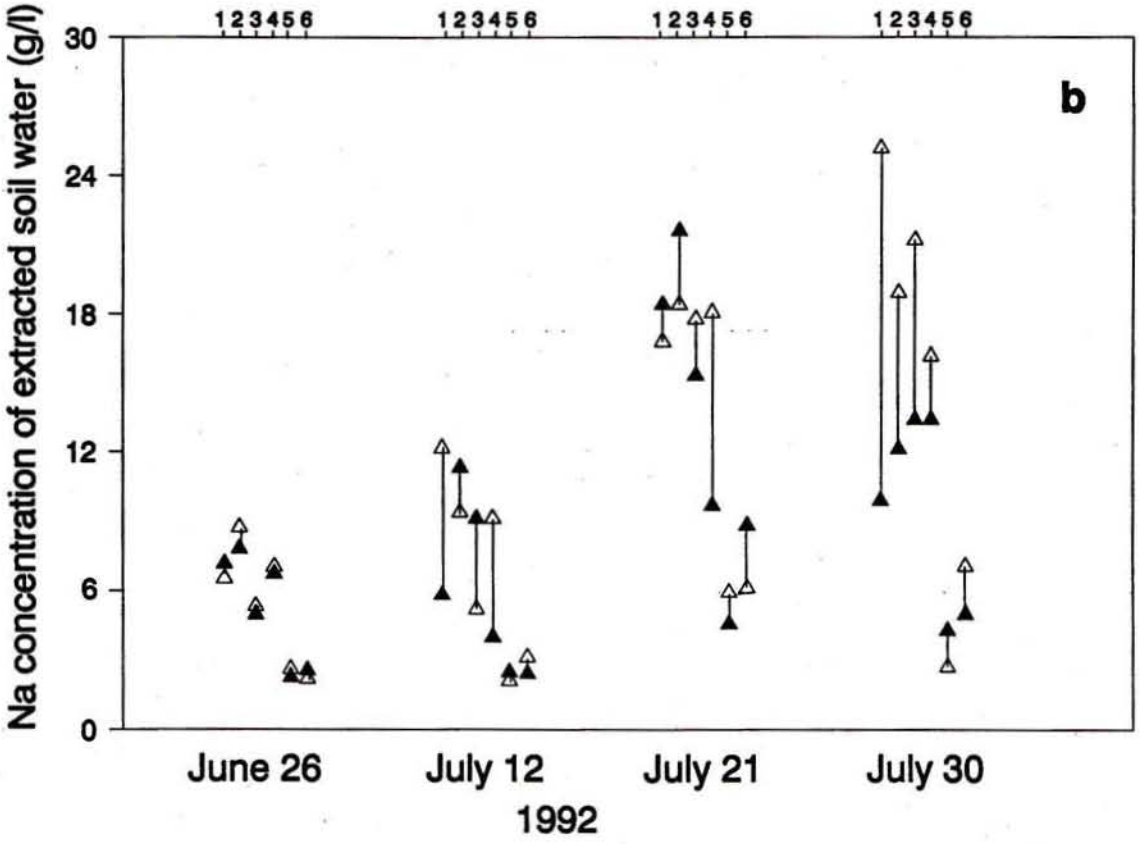
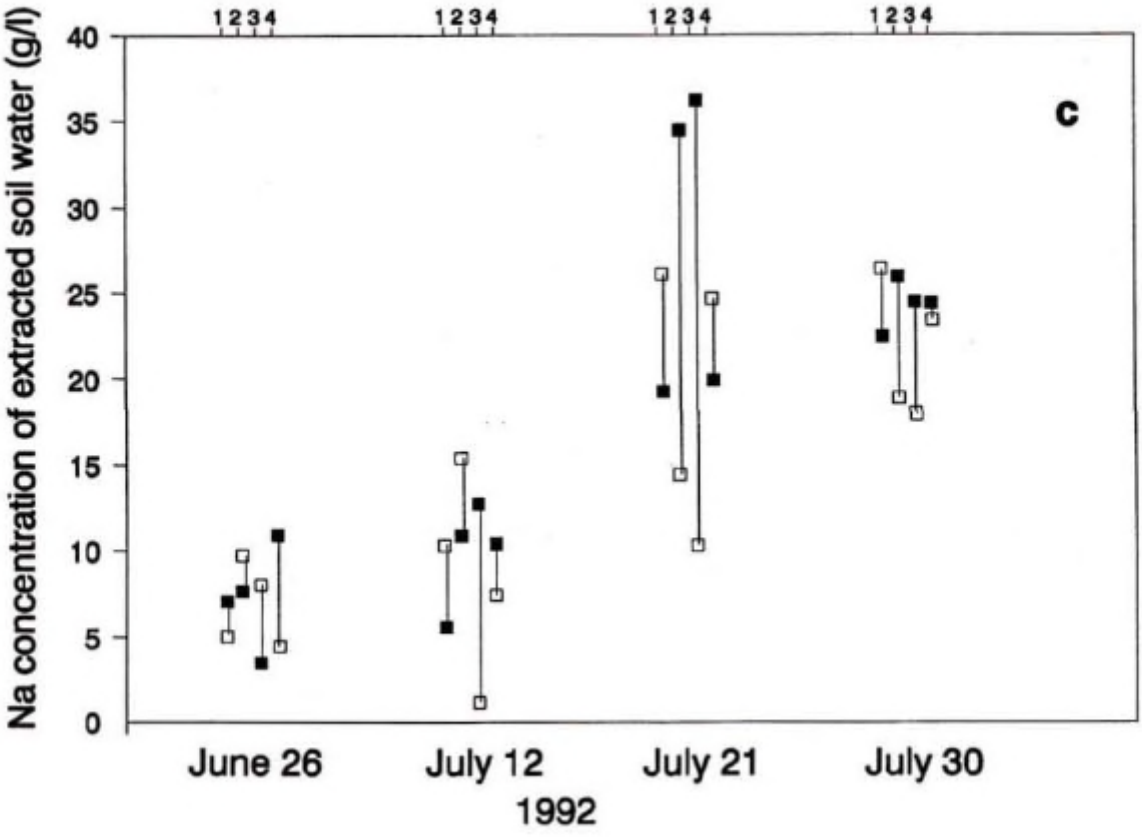
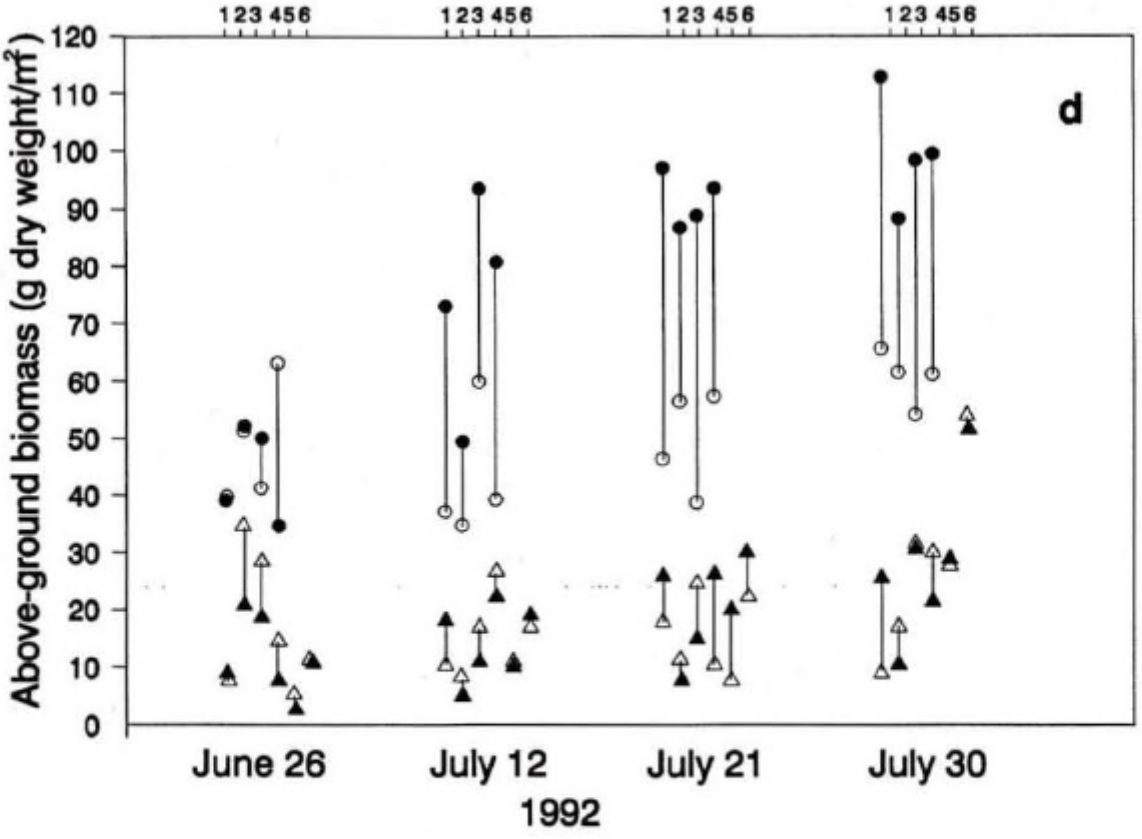


Fig. 5.4. Sodium concentration in soil water (a,b,c) and above-ground biomass (d) of grazed (open symbols) and exclosed (closed symbols) areas of sites. Sites (numbered) represented either high biomass (circles), low biomass (triangles), or bare (squares) vegetation. All areas were exclosed on June 26, 1992. Note that the vertical axes differs between (a), (b), and (c). The biomass of bare sites was negligible and so is not shown in (d).


1 2 3 4
1 2 3 4
1 2 3 4
1 2 3 4
a
Na concentration of extracted soil water (g/l)
0
1
2
3
4
5
6
June 26
July 12
July 21
July 30
1992


1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
b
Na concentration of extracted soil water (g/l)
0
6
12
18
24
30
June 26
July 12
July 21
July 30
1992


1 2 3 4
1 2 3 4
1 2 3 4
1 2 3 4
Na concentration of extracted soil water (g/l)
0
5
10
15
20
25
30
35
40
c
June 26
July 12
July 21
July 30
1992


1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
Above-ground biomass (g dry weight/m²)
0
10
20
30
40
50
60
70
80
90
100
110
120
d
June 26
July 12
July 21
July 30
1992

grazed high biomass areas.

The sodium concentration in extracted soil-water is a measure of soil salinity (Chapter 4). Grazed areas were more saline than exclosed areas in all high biomass sites and on all post-exclosure dates (July 12, July 21, and July 30). In low biomass sites, differences in salinity between grazed and exclosed areas were not consistent between sites and dates, although grazed areas tended to be more saline on July 30. In bare sites, there were no consistent differences between areas available for grazing and exclosed areas. Soil salinity increased throughout the study period in all biomass categories. On all dates, bare sites were more saline than low biomass sites, and the latter were more saline than high biomass sites. Notably, the salinity of low biomass sites 5 and 6 was closer to that of high biomass sites than that of the other four (more representative) low biomass sites.

In summary, exclosing areas from grazing appears to decrease soil salinity when it also results in a biomass increase (ie. in high biomass sites). Low biomass and bare sites serve as a control, since their exclosure does not affect biomass. Although grazed areas were more saline in all four representative low biomass sites (sites 1 to 4) on July 30, there is a 18% probability of this occurring on at least one of the post-exclosure dates by chance alone. By comparison, there is a 0.024% chance of grazed areas being more saline in all sites on all post-exclosure dates (as in high biomass sites).

Other soil variables measured included redox potential (E_h values), bulk density, and gravimetric water content. Soils from high biomass sites tended to be wetter and less dense (highly correlated: Chapter 4) than soils from low biomass or bare sites. Exclosed areas in high biomass sites and those in low biomass sites 5 and 6 also tended to have wetter and less dense soil than their grazed counterparts (Table 5.2). Soil redox potential did not exhibit such trends.

Relationships among soil variables and biomass were examined by comparing average values (mean of all four dates) for each area (n=28: low biomass sites 5 and 6

Table 5.2. Soil variables measured on July 30, 1992, in grazed (gr) and exclosed (ex) areas of high biomass (H), low biomass (L), and bare (B) sites. Site numbers correspond to those in Fig. 5.4.

Site	Soil water content (g_{water}/g_{soil})	Soil bulk density (g/cm^3)	Soil redox potential (mV)
H1 gr	0.586	0.917	120
ex	0.754	0.853	125
H2 gr	0.640	0.747	135
ex	0.750	0.705	115
H3 gr	0.674	0.826	125
ex	0.794	0.695	140
H4 gr	0.709	0.722	140
ex	0.803	0.752	140
L1 gr	0.533	1.091	110
ex	0.606	0.896	170
L2 gr	0.605	1.060	75
ex	0.472	1.121	130
L3 gr	0.493	1.077	145
ex	0.499	0.908	140
L4 gr	0.571	1.023	130
ex	0.479	0.967	140
L5 gr	0.586	0.736	145
ex	0.779	0.692	180
L6 gr	0.660	0.989	130
ex	0.781	0.839	85
B1 gr	0.460	0.988	135
ex	0.599	1.007	105
B2 gr	0.520	0.903	125
ex	0.629	0.922	120
B3 gr	0.584	1.066	130
ex	0.619	1.007	130
B4 gr	0.375	1.105	125
ex	0.602	0.946	95

included). Although different areas of the same site are not truly independent, the above discussion suggests that exclosing areas can cause radically different edaphic conditions, simulating independence. Average biomass and average sodium concentration in soil water (logarithmic form) were highly and negatively correlated ($r=-0.85$, $p<0.001$: Fig 5.5), corroborating previous results (Chapter 4). Average water content and bulk density were also highly and negatively correlated ($r=-0.86$, $p<0.001$). Weaker correlations existed between these two sets of almost colinear variables (r from 0.40 to 0.60, $p<0.05$). Average redox values were uncorrelated with all variables, except a spurious correlation with bulk density ($r=-0.574$) caused by one exceptionally reduced (E_h value=50 mV) soil on July 12.

The average sodium concentration was highly predictable from a linear regression equation including the biomass on July 21 and July 30, and bulk density of July 21 and July 30 ($r^2 = 0.83$; stepwise regression, p enter = 0.15). Variables entered into the stepwise regression were redox, water content, bulk density and biomass for each date and their season averages. Notably, this equation includes values for only the last two dates, suggesting that differences between sites in biomass or soil variables were too small or variable on earlier dates to predict salinity. In individual stepwise regressions for each date, biomass was consistently the main explanatory variable for sodium concentrations with only water content on June 26 and bulk density on July 30 entering as secondary explanatory variables (r^2 from 0.40 to 0.77).

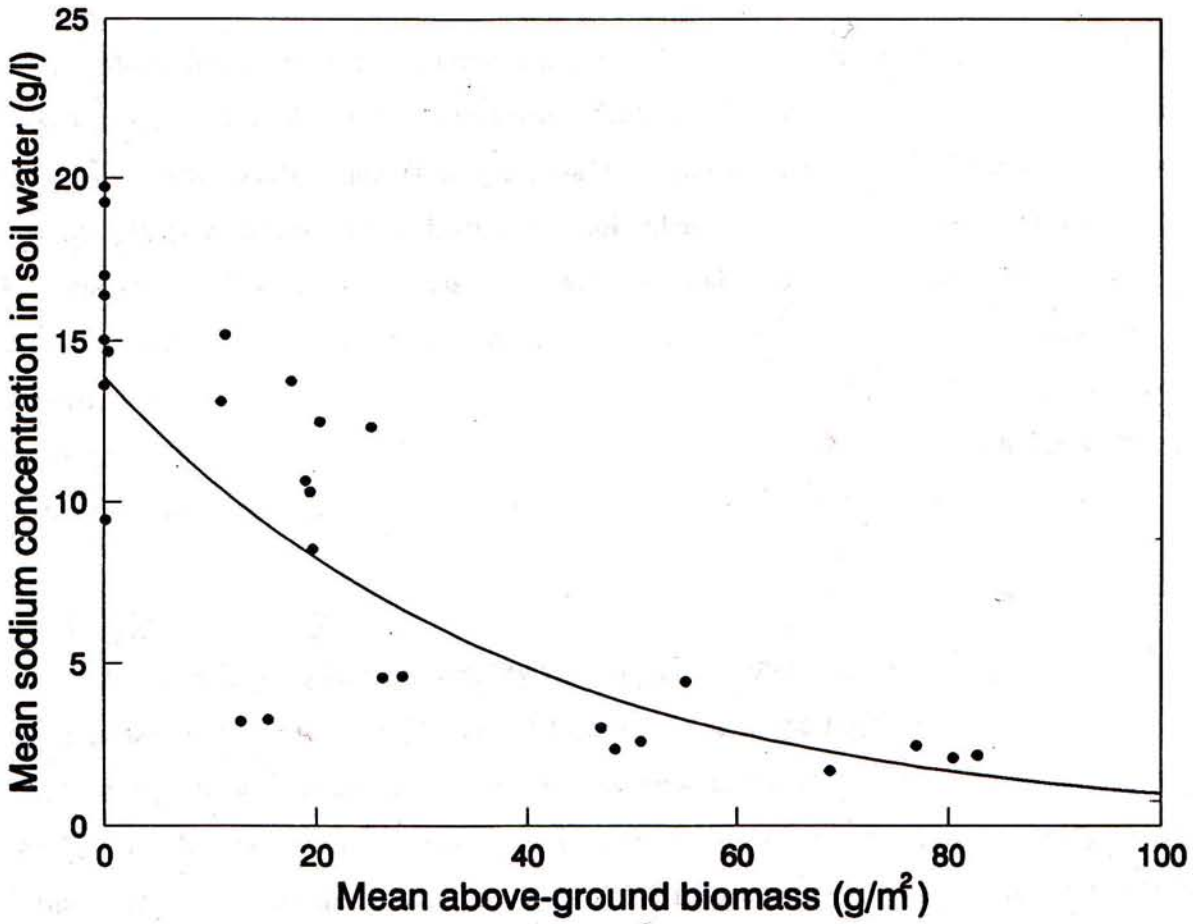
These relationships between soil variables corroborate results discussed earlier (Chapter 4), and indicate that exclosing high biomass swards does affect soil salinity and soil moisture.

5.5.2. Plant mortality and axillary shoot production differed between biomass categories and between years.

5.5.2.1 1991

Data were divided into four treatment classes (n=56 plants/treatment) based on site

Fig. 5.5. Sodium concentration in soil water as a function of site biomass for sites in 1992. The regression line was calculated for an exponential form of biomass.



biomass and sodium concentration in extracted soil water: high biomass (0 to 2 g/l Na^+), low biomass (0 to 2 g/l Na^+), low biomass (2 to 4 g/l Na^+), and low biomass (4 to 8 g/l Na^+).

Overall, a greater proportion of plants in low biomass sites (58%) produced axillary shoots than in high biomass sites (41%). In low biomass sites, the percentage of plants producing axillary shoots decreased from 73% in less saline sites (0 to 2 g/l Na^+) to 61% in sites of intermediate salinity (2 to 4 g/l Na^+) to 39% in the most saline sites (4 to 8 g/l Na^+).

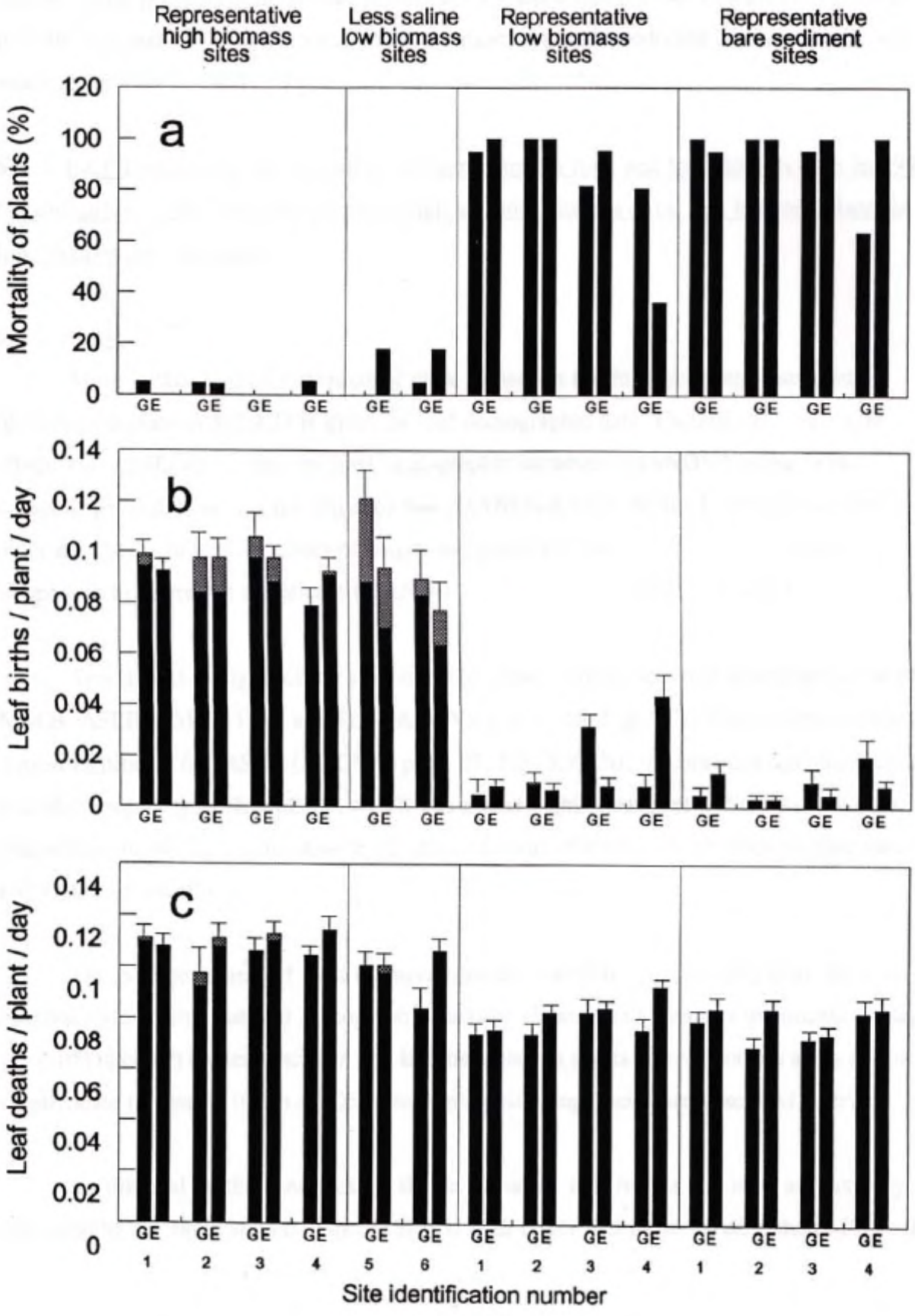
Mortality of main shoots increased from 5% in high biomass sites to 13% in low biomass sites of low and intermediate soil salinity (0 to 2, and 2 to 4 g/l Na^+) to 22% in the most saline low biomass sites (4 to 8 g/l Na^+). Axillary shoots continued to grow in about half the plants with dead main shoots, so whole plant mortality increased from 4% in high biomass sites to 7% in low biomass sites with low and intermediate soil salinity (0 to 2, and 2 to 4 g/l Na^+) to 14% in the most saline low biomass sites (4 to 8 g/l Na^+). By mid-August, 1991, 85% of the most saline low biomass sites (4 to 8 g/l Na^+) had noticeable yellowing of (non-transplanted) graminoids, indicating early senescence. Similar yellowing of plants was not observed in any other high or low biomass site.

5.5.2.2 1992

In general, *Puccinellia* mortality was higher in 1992 than 1991 (Fig. 5.6.a). Mortality of transplanted *Puccinellia* plants varied from 0 to 3% in the high biomass sites, from 58 to 100% in the (four representative) low biomass sites, and from 82 to 100% in bare sites. In the two low biomass sites of below average salinity (sites 5 and 6, the latter being more saline: Fig 5.4.b), mortality was only 9 and 12% respectively. Detailed analyses of the role of biomass and soil salinity in causing plant mortality are described later.

Only 10% of high biomass plants produced axillary shoots, while no plants in bare areas and only 1 plant in a (representative) low biomass site (<1% of low biomass plants) produced axillary shoots. In the two low biomass sites of below average salinity, 32% of plants produced axillary shoots. These results are the reverse of results in 1991, when

Fig. 5.6. *Puccinellia* plant mortality (a), total leaf birth rate (b), and total leaf death rate (c) in grazed (G) and exclosed (E) areas of sites in 1992. Leaves on main shoots are represented by solid bars, and leaves on axillary shoot leaves by hatched bars. Sites numbering corresponds to that in Fig. 5.4. Error bars are $\pm$ 1 SE.


Representative high biomass sites
Less saline low biomass sites
Representative low biomass sites
Representative bare sediment sites
a
b
c
Mortality of plants (%)
Leaf births / plant / day
Leaf deaths / plant / day
GE
Site identification number

axillary shoot production in average low biomass areas exceeded that in high biomass areas. In both high and low biomass sites, the percentage of plants producing axillary shoots was much lower than in 1991.

5.5.3. Leaf demography did not differ between plants in high and low biomass sites in 1991, but did differ in 1992 between plants in high and low biomass sites, and between plants in low biomass and bare sites.

5.5.3.1 1991

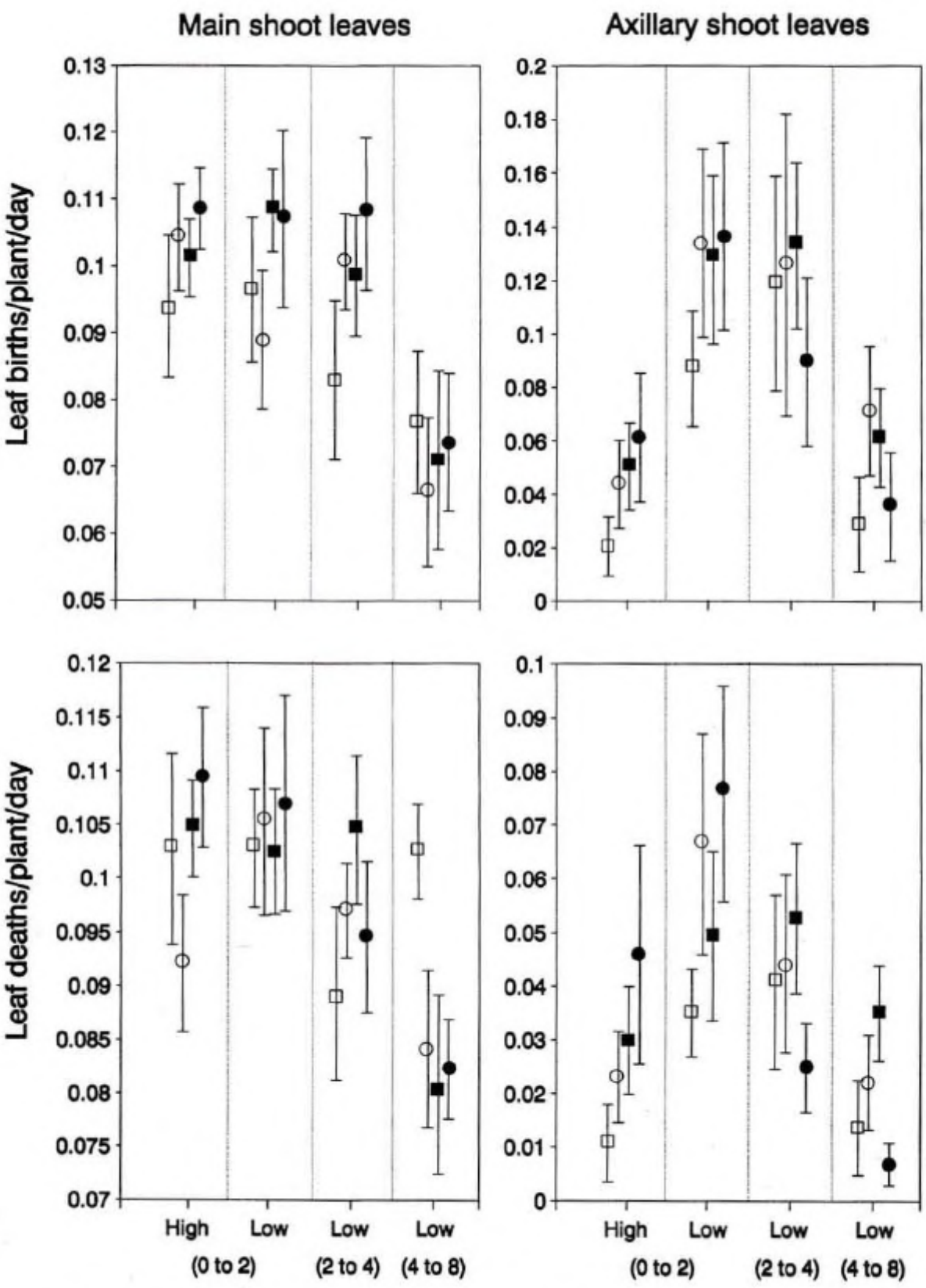
More detailed characterization of plant growth in the four treatment categories (described in section 5.5.2.1) is given by leaf demographic data. Overall, this treatment effect was significant for the seasonal demographic variables (MANOVA using Wilks Lambda, $p<0.03$), as was the effect of site (MANOVA using Wilks Lambda, $p<0.001$). All other effects, including the effect of origin and grazing, and all possible interactions (Appendix 1), were not significant (MANOVA using Wilks Lambda, $p>0.05$).

Specifically, a significant treatment effect existed for the seasonal demographic variables MSLB, ASLB, ASLD, TLB, and TLD (ANOVAs, $p<0.05$; Fig. 5.7). This treatment effect was almost significant for MSLD (ANOVA, $p<0.07$; Fig. 5.7). All seasonal demographic variables had also a significant effect of site, which was nested within treatment (ANOVAs, $p<0.05$). No interactions involving treatment were significant for any of these seasonal demographic variables (ANOVAs, $p>0.05$).

On average, plants of high biomass sites did not differ significantly from those of low biomass sites in any seasonal demographic variable (F tests, low biomass treatments averaged, $p>0.05$) although the tendency for ASLB to be higher in plants of low biomass areas approched significance (F test, $0.10>p>0.05$). Other planned comparisons are described later.

In this and further analyses, it should be noted that results for total and axillary leaf demography are often similar. Since ASLB is both larger and more variable than MSLB (Fig

Fig. 5.7. Seasonal-based leaf demographic parameters of *Puccinellia* plants of high biomass origin (□,■) and low biomass origin (○,●), in grazed (□,○) and exclosed (■,●) areas of sites in 1991. Dotted lines separate sites in different treatment categories (based on site biomass and the sodium concentration of soil-water). Demographic parameters were calculated for the period June 11 - August 9, 1992. Error bars are $\pm$ 1 SE. Note that the vertical axes are not identical.


Main shoot leaves
Axillary shoot leaves
Leaf births/plant/day
Leaf deaths/plant/day
0.13
0.12
0.11
0.1
0.09
0.08
0.07
0.06
0.05
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
0.12
0.115
0.11
0.105
0.1
0.095
0.09
0.085
0.08
0.075
0.07
0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
High
Low
Low
Low
(0 to 2)
(2 to 4)
(4 to 8)
Site biomass (high or low) and sodium concentration of soil water (g/l)

5.7), TLB tends to be more highly correlated with ASLB ($r=0.95$, $n=224$) than with MSLB ($r=0.46$). Similarly, TLD is more highly correlated with ASLD ($r=0.91$) than with MSLD ($r=0.62$).

5.5.3.2 1992

Leaf demography was examined in four representative sites of each biomass category. Since axillary shoot production was low, only total (main shoot + axillary shoot) leaf demography was examined. Both TLB and TLD varied considerably between sites (Friedman test, sites not differentiated by biomass category, $p<<0.001$; Fig. 5.6.b,c). Planned multiple comparisons indicated that TLB and TLD are both higher in high biomass sites than in other (low biomass and bare) sites, and that TLB is higher in low biomass sites than in bare sites (Wilcoxon Rank Sum, Z-statistic, $p<0.05$). Values of TLD are not significantly different between low biomass and bare sites (Wilcoxon Rank Sum, Z-statistic, $p>0.05$). Within each biomass category, this site effect was greatest for TLB and TLD of plants from low biomass sites and was only significant for TLB of plants from low biomass sites (Friedman tests for each biomass category, $p<0.05$).

5.5.4. Grazing and plant origin had complex effects on leaf demography in 1991, and grazing increased leaf deaths in 1992.

5.5.4.1 1991

As noted in section 5.5.3.1, the effect of grazing was not significant overall (MANOVA using Wilks Lambda, $p<0.10<0.05$). The effect of origin and all possible interactions involving grazing and origin were also not significant (MANOVA using Wilks Lambda, $p>0.25$).

Exclosure of plants from grazing, however, increased ASLD significantly (ANOVA, $p<0.03$) and tended to increase ASLB and MSLB, although the latter two comparisons only approached significance (ANOVAs, $0.09<p<0.07$; however, see section 5.5.7.1 for a MSLB grazing x salinity interaction). For both ASLB and ASLD, a significant interaction

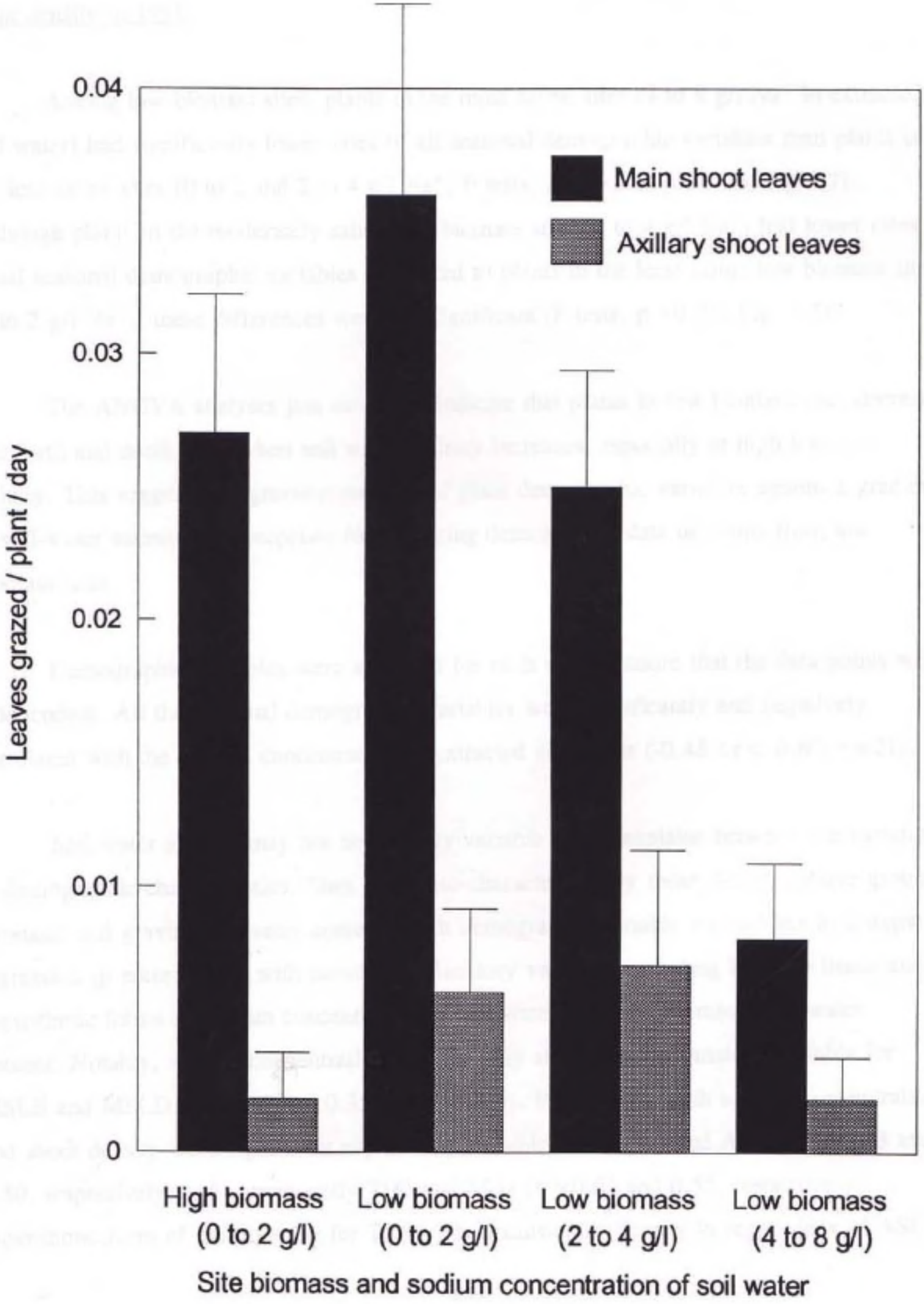
existed between plant origin and grazing category (ANOVAs, $p<0.04$): although plants of high biomass origin tended to have higher rates of ASLB and ASLD when exclosed from grazing, the reverse was true for plants of low biomass origin (Fig 5.7). The interaction between origin and site was just significant for TLD (ANOVA, $p<0.05$): plants of high biomass origin have higher rates of TLD than those of low biomass origin in 11 of the 28 sites, but mainly in the less saline sites (high biomass origin plants have higher TLD than low biomass origin plants in 7 of 14 sites with 0 to 2 g/l Na^+ in extracted soil water).

It should be noted that the grazing rate is not uniform among treatments or shoot type, and even within treatments and shoot types it is highly variable (Fig. 5.8). The grazing rate of main shoot leaves was highest in low biomass sites of low salinity (0 to 2 g/l Na^+), very low in the most saline low biomass sites (4 to 8 g/l Na^+) and intermediate in the other treatments. These differences in grazing rates may reflect differences in numbers of live main shoot leaves among treatments, "dilution" of herbivory in high biomass sites, or preference for younger or less salty leaves by geese. The grazing rate of axillary shoot leaves is much lower than that of main shoot leaves in all treatments, even in less saline low biomass sites (0 to 2 g/l Na^+) where almost all plants had axillary shoots. The relative proximity of axillary shoot leaves to the soil surface may protect them from grazing.

5.5.4.2 1992

The effect of grazing is not significant for TLB, but TLD of plants is higher in exclosed areas (Friedman test, sites not differentiated by biomass category, $p<0.01$). It is not possible to test explicitly for interaction in the non-parametric Friedman test (Miller, 1966), unless populations have a similar and describable underlying distribution function (Cambell and Skillings, 1985). It should be noted, though, that a large difference in TLD of plants in exclosed and grazed areas occurs only in one bare site (Fig. 5.6.c). In individual analyses of each biomass category, this effect of grazing was greatest and almost significant in plants from low biomass areas (Friedman test, $p<0.06$), but not significant in plants from high biomass or bare areas (Friedman tests, $p>0.10$).

Fig. 5.8. Grazing rate of leaves on main and axillary shoots on *Puccinellia* plants in 1991. Plants were divided into four treatments based on site biomass and sodium concentration of soil water. Error bars are $\pm$ 1 SE. Note that a high number of leaves grazed per plant in a treatment could indicate either a herbivore preference for plants of that treatment, or a large number of leaves available for grazing per plant in that treatment.


0.04
0.03
0.02
0.01
0
Leaves grazed / plant / day
Main shoot leaves
Axillary shoot leaves
High biomass (0 to 2 g/l)
Low biomass (0 to 2 g/l)
Low biomass (2 to 4 g/l)
Low biomass (4 to 8 g/l)
Site biomass and sodium concentration of soil water

5.5.5. Within the low biomass sites, leaf demography was a function of both salinity and plant density in 1991.

Among low biomass sites, plants in the most saline sites (4 to 8 g/l Na^+ in extracted soil water) had significantly lower rates of all seasonal demographic variables than plants in the less saline sites (0 to 2 and 2 to 4 g/l Na^+; F tests, $F_{1,24} > 5.3$, $p < 0.05$; Fig 5.7). Although plants in the moderately saline low biomass sites (2 to 4 g/l Na^+) had lower rates of all seasonal demographic variables compared to plants in the least saline low biomass sites (0 to 2 g/l Na^+), these differences were not significant (F tests, $p > 0.05$; Fig. 5.7).

The ANOVA analyses just described indicate that plants in low biomass sites decrease leaf birth and death rates when soil water salinity increases, especially at high levels of salinity. This suggests a regression analysis of plant demographic variables against a gradient of soil-water salinity is appropriate for analyzing demographic data of plants from low biomass sites.

Demographic variables were averaged for each site to ensure that the data points were independent. All the seasonal demographic variables were significantly and negatively correlated with the sodium concentration of extracted soil water ($-0.48 < r < -0.60$, $n=21$).

Soil-water salinity may not be the only variable which explains between-site variation in demographic characteristics. Sites were also characterized by shoot density, above-ground biomass, and gravimetric water content. Each demographic variable was subject to a stepwise regression (p enter=0.15) with possible explanatory variables including both the linear and logarithmic forms of sodium concentration of soil water, density, biomass, and water content. Notably, sodium concentration was the only significant explanatory variable for MSLB and MSLD ($r^2=0.30$ and 0.35, respectively). By contrast, both sodium concentration and shoot density were significant explanatory variables for ASLB and ASLD ($r^2=0.53$ and 0.50, respectively) and consequently TLB and TLD ($r^2=0.63$ and 0.55, respectively; logarithmic form of density used for TLB). The inclusion of density in regressions of ASLB,

ASLD, TLB and TLD with just sodium concentration as an explanatory variable increases the r^2 from ca. 0.30 to ca. 0.55. Density of shoots, therefore, appears to be important in axillary leaf demography, but not main shoot leaf demography. The stepwise regressions with interval-based demographic parameters confirm this conclusion (Appendix 2). In all regression equations, the effect of increasing sodium concentration or shoot density was a decrease in the demographic parameter.

Similar regression analyses are not suitable for the data of 1992 since only six low biomass sites were examined. Note, however, that *Puccinellia* plants in low biomass sites of below-average salinity (sites 5 and 6) had much higher TLB and TLD rates than plants in the more representative low biomass sites (Fig 5.6).

5.5.6. Within sites of similar soil salinity, leaf demography of axillary shoots was a function of plant density.

5.5.6.1 1991

High and low biomass sites of the same salinity (0 to 2 g/l Na^+) can be compared, although this comparison is not analyzed statistically as it is not orthogonal to three comparisons described earlier (sections 3.1, 5.1; statistical analysis would reduce power considerably of previous comparisons). Compared with high biomass sites, these low biomass sites had six-fold greater ASLB (0.0365 vs 0.0061 leaves/plant/d) and four-fold greater ASLD (0.0182 vs. 0.0047 leaves/plant/d). Differences between high and low biomass sites (0 to 2 g/l Na^+) in MSLB and MSLD were small by comparison.

5.5.6.2 1992

Soil salinity of low biomass sites 5 and 6 was similar to that of the high biomass sites (Fig 5.4). *Puccinellia* plants in low biomass sites 5 and 6 have a similar TLD to plants in high biomass sites, and a slightly higher TLB than plants in the high biomass sites (Fig 5.7). The latter is due to a greater ASLB in plants in low biomass sites 5 and 6 than in plants in the high biomass sites. This trend is analyzed in further in section 7.2 and Appendix 2.

5.5.7. Regression analyses involving sites from all biomass categories indicated that both salinity and density were important determinants of leaf demography in both 1991 and 1992.

5.5.7.1 1991

In the low biomass sites, plant growth appears to be dependent on gradients of soil-water salinity and of shoot density. The shoot density gradient can be extended by inclusion of high biomass sites. Again, average demographic values were used for each site to ensure data points were independent. Demographic data from two additional high biomass sites (2.7 and 3.0 g/l Na in soil water) were included to increase the number and variety of high biomass sites.

Stepwise regressions (p enter=0.15) were again performed with explanatory variables including biomass category (1=high biomass, 0=low biomass) and the linear, logarithmic, and quadratic forms of sodium concentration in extracted soil water, gravimetric water content, shoot density, and above-ground biomass. Note that shoot density, biomass, and biomass category are all intercorrelated ($0.59<r<0.93$), and are essentially different measurements of the same dichotomy of high biomass and low biomass sites. The resultant regression equations (Table 5.3) can be summarized as follows. Sodium concentration is the only explanatory variable for MSLB and MSLD. Both sodium concentration and shoot density are significant explanatory variables for ASLB, ASLD, TLB, and TLD. As in the regression analysis of just the low biomass sites, axillary shoot demography is more dependent on density than are the demographic variables for main shoot leaves.

Although the effect of density in these regression equations is non-linear for many demographic variables, ASLB, ASLD, TLB and TLD generally decrease as density increases (at least for the range of densities examined: ie., from 0.2 to 6.9 plants/cm^2). The effect of sodium concentration in all regression equations was a decrease in leaf birth and death rates.

It could be argued that by averaging data for all eight plants per site, important

Table 5.3. Regression equations explaining seasonal leaf demographic parameters (see text for units and abbreviations) in terms of site variables. Significant site variables include sodium concentration in soil water (Na), plant density (density), above-ground biomass (biomass), and grazing category (graze: 0=exclosed, 1=grazed). In 1991, all terms are significant at a 15% significance level, while in 1992, results at both a 5% and 15% significance level are given for reasons discussed in the text.

Demographic parameters in 1991

$MSLB = 0.1104 - 0.006077(Na)$ $r^2=0.34$

$MSLD = 0.1071 - 0.02596(\log_{10}Na)$ $r^2=0.35$

$ASLB = 0.07138 + 0.03254(density) - 0.2704(\log_{10}density) - 0.002519(Na^2)$ $r^2=0.64$

$ASLD = 0.0592 - 0.00944(Na) - 0.07542(\log_{10}density) + 0.001230(density^2)$ $r^2=0.51$

$TLB = 0.2030 - 0.2369(\log_{10}density) - 0.003368(Na^2) + 0.004017(density^2)$ $r^2=0.65$

$TLD = 0.1679 - 0.01375(Na) - 0.08924(\log_{10}density) + 0.001574(density^2)$ $r^2=0.52$

Demographic parameters in 1992

$Mortality\ (15\%,5\%) = -0.923 + 6.747(\log_{10}Na)$ $r^2=0.68$

$TLB\ (15\%) = 5.853 - 0.01304(biomass) + 0.01020(graze \times biomass) - 4.658(\log_{10}Na)$ $r^2=0.93$

$TLB\ (5\%) = 5.931 - 0.01382(biomass) - 4.726(\log_{10}Na)$ $r^2=0.93$

$TLD\ (15\%,5\%) = 4.055 - 0.1828(graze) - 1.107(\log_{10}Na)$ $r^2=0.83$

$MSLB\ (15\%) = 4.235 + 0.2200(graze) + 0.0113(graze \times biomass) - 3.427(\log_{10}Na)$ $r^2=0.92$

$MSLB\ (5\%) = 4.343 - 3.425(\log_{10}Na)$ $r^2=0.91$

$MSLD\ (15\%) = 4.003 - 0.1845(graze) - 1.123(\log_{10}Na)$ $r^2=0.81$

$MSLD\ (5\%) = 3.930 - 1.140(\log_{10}Na)$ $r^2=0.77$

information on the effect of grazing and the site of plant origin is lost. To examine this possibility, regression models were computed for plants differentiated by their grazing status and origin in each site. Independent variables including grazing effect (categorical; 1=grazed area 0=exclosed), origin (categorical; 1=low biomass origin, 0=high biomass origin), either or both sodium concentration and density (as appropriate, linear or logarithmic form), and all possible interactions (except the density by sodium concentration interaction which is not appropriate given the degree of collinearity between these two variables). For most demographic variables, only the site variables (density and/or sodium concentration) were significant. A grazing by sodium concentration interaction (in addition to the previously discussed grazing effect) was significant for MSLB. As is evident in Fig. 5.7, grazing reduces main shoot leaf births primarily in less saline sies (0 to 2 g/l Na^+) and has little effect in the more saline sites (4 to 8 g/l Na^+). This interaction is analogous to a grazing by treatment interaction found for MSBR (Appendix 2).

5.5.7.2 1992

Both biomass and soil salinity, in addition to other soil variables, differed between the categories of high biomass, low biomass, and bare sites. These soil variables and biomass are not, however, absolutely colinear, especially when data from the two low biomass sites with below average soil salinity (sites 5 and 6) are included. It is therefore possible to separate the effects of biomass and salinity by regression analyses. Again, regression analyses are performed using each area as an independent data point; although grazed and exclosed areas within the same site are not truly independent, they often have very different edaphic conditions. Average values of TLB and TLD were used for each area.

Dependent variables in this regression analysis included TLB, TLD, and whole plant mortality (%). Possible explanatory variables included the season average of each of above-ground plant biomass, sodium concentration in soil-water, soil redox potential, water content of soil, and bulk density of soil (all expressed in both linear and logarithmic form) as well as exposure to grazing (categorical variable: 1=grazed area 0=exclosed area), and the interaction between grazing and each of the other variables (both linear and logarithmic

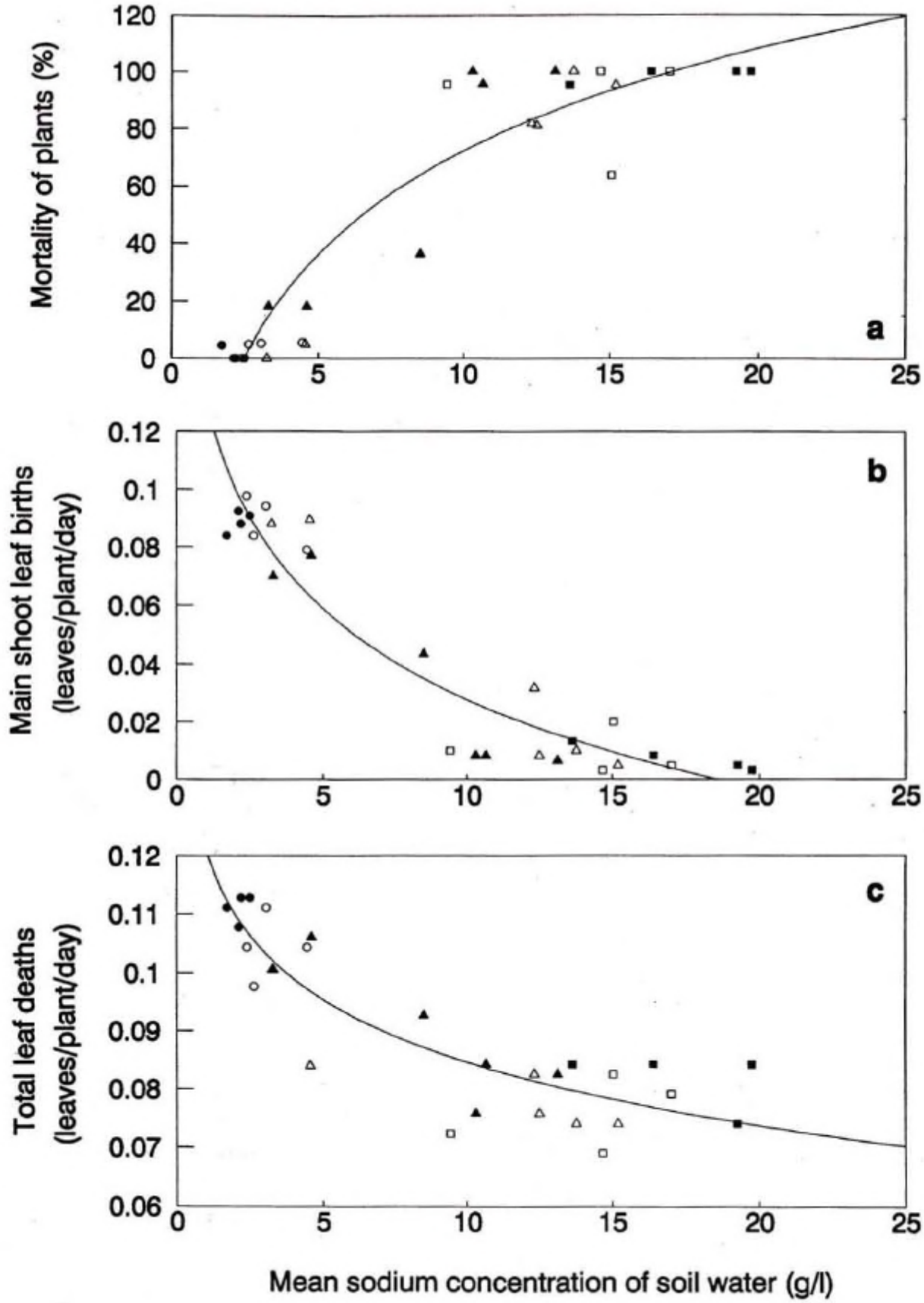
forms). This model therefore allows biomass and soil variables to be treated as covariates in the analysis of grazing effect. Stepwise regression was used to select important explanatory variables (p enter = 0.15; Table 5.3). To facilitate interpretation of the results, interactions were allowed only with the same form (linear or logarithmic) of biomass or soil variables which entered into the stepwise regression equation.

The only significant ($p<0.15$) explanatory variable for whole plant mortality (%) over the study period was average sodium concentration (logarithmic form, $r^2=0.85$; Table 5.3; Fig 5.9.a). Even plant mortality in the first interval could be explained (only) by average sodium concentration (logarithmic form, $r^2=0.68$). In both cases, increasing salinity increased plant mortality.

The only two significant explanatory variables for TLD were average sodium concentration (logarithmic form, $p=0.0001$) and the effect of grazing ($p=0.0247$), together explaining 83.2% of variance in TLD (Table 5.3; Fig 5.9.c) The effect of both increasing sodium concentration and grazing on TLD was negative (ie., plants in exclosed areas of low salinity had the highest TLD). This result is consistent with the importance of grazing and biomass category in earlier analyses (Friedman tests).

Significant explanatory variables for TLB included average sodium concentration (logarithmic form, $p<0.0001$), average biomass (linear form, $p<0.025$), and the interaction between grazing and biomass ($0.10<p<0.15$). Note that the interaction between grazing and biomass is not significant at a 5% probability level, and removal of this term has little effect on the fit of the model (r^2 decreases from 0.933 to 0.926; Table 5.3). In either model, an increase in sodium concentration or biomass both reduce TLB. (The interaction between grazing and biomass causes higher TLB in grazed areas than exclosed areas of high biomass sites, but no difference in bare sites). In earlier analyses, biomass category but not grazing was important (Friedman tests). The significance of biomass as an explanatory variable for TLB can be explained as greater axillary shoot leaf production in low density sites of below average salinity than in high biomass sites. If the above model is rerun with MSLB in place

Fig. 5.9. Mortality (a), main shoot leaf birth rate (b), and total leaf death rate (c) of *Puccinellia* plants as a function of sodium concentration in soil-water. Plants were in grazed (open symbols) or exclosed (closed symbols) areas of sites in either high biomass (circles), low biomass (triangles), or bare (squares) vegetation. Each symbol in (b) and (c) represents the mean of 18 plants. Regression lines are calculated using a logarithmic form of sodium concentration. Main shoot leaf birth rate is shown rather than total leaf birth rate as the latter is also influenced by biomass (see text). Note that exclosed plants tend to have higher leaf death rates than grazed plants in sites of a given biomass, reflecting the importance of grazing level in regression equations involving total leaf death rates (see text).


Mortality of plants (%)
120
100
80
60
40
20
0
0
5
10
15
20
25
a
Main shoot leaf births (leaves/plant/day)
0.12
0.1
0.08
0.06
0.04
0.02
0
b
Total leaf deaths (leaves/plant/day)
0.12
0.11
0.1
0.09
0.08
0.07
0.06
c
Mean sodium concentration of soil water (g/l)

of TLB, the only variable significant at a 5% level is average sodium concentration ($p=0.0001$, $r^2=0.91$; Table 5.3; Fig 5.9.b). Results for MSLD are similar to those for TLD (Table 5.3). As in 1991, both salinity and density are important in axillary shoot demography, but only salinity is important in main shoot demography.

5.5.8. Carex growth was also greater in high biomass areas than in bare areas

All *Carex* plants died in all four bare sites (grazed areas) by the end of the first interval. By contrast, plant mortality over the entire study period varied from 17 to 37% in the four high biomass sites (grazed areas). *Carex* was not transplanted in exclosed areas. Clearly, growing conditions were more adverse for *Carex* in bare sites than high biomass sites.

In grazed areas of high biomass sites, *Puccinellia* mortality by the end of the study period was consistently lower than that of *Carex* (0% vs. 17%, 5% vs. 29%, 0% vs. 24%, 6% vs. 37% for high biomass sites 1,2,3,4 respectively). Note that both *Puccinellia* and *Carex* mortality are lowest, intermediate, and highest in the same sites. The grazed area of high biomass site 4, which had the highest mortality rate for both species, was more saline on all dates than the grazed areas of other high biomass sites (Fig 5.4.a). In grazed areas of bare sites, by the end of the first interval, *Puccinellia* mortality was 48%, 100%, 91%, and 30% for sites 1 to 4, respectively. *Puccinellia* mortality was therefore generally lower than *Carex* mortality in bare sites in the first interval (*Puccinellia* plants were still alive in two of the bare sites by the end of the study period, too).

Average values of TLB for *Carex* plants in high biomass sites varied from 0.0182 to 0.0506 leaves/plant/day, depending on site (site effect significant, ANOVA, $p<0.05$), compared to values of 0.0791 to 0.106 leaves/plant/day for *Puccinellia* (same grazed areas). This difference in TLB between *Carex* and *Puccinellia* corroborates differences in plant mortality discussed above.

There was no significant difference in TLD of *Carex* plants between high biomass sites (ANOVA, $p>0.80$). On average ($\pm$ SE), the TLD of *Carex* plants in high biomass sites was 0.0489 ($\pm$ 0.0005) leaves/plant/day, much less than corresponding values for *Puccinellia* in high biomass sites (Fig 5.6.c). This does not imply that *Carex* is healthier because its leaves are dying more slowly. Rather, it indicates that *Carex* leaf death rates were limited by the production of new leaves, especially after widespread mortality of *Carex* plants occurred early on in the study.

Two possible explanations for the higher *Carex* mortality (and associated poor growth) in both high biomass and bare sites relative to *Puccinellia* plants are a) *Carex* is more salt-sensitive than *Puccinellia*, so even in high biomass areas it had considerable mortality, and b) *Carex* is more sensitive to stress associated with transplanting. At this point, neither explanation can be discounted.

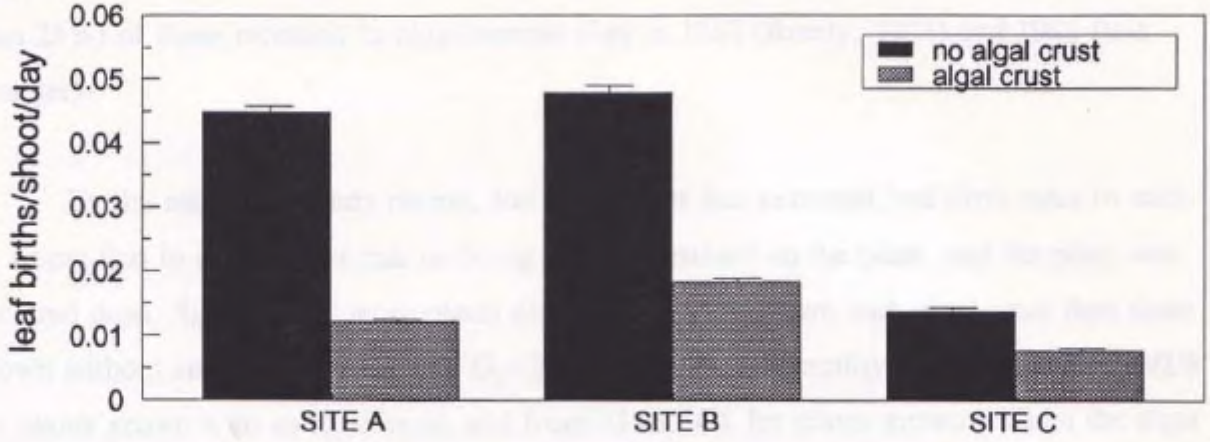
5.5.9. Algal crusts reduced *Puccinellia* growth in bare areas

The total leaf birth rate (TLB) was significantly lower for plants grown in intact algal crust, compared to plants grown with algal crust removed (Friedman test, $p<0.001$). Plants grown in algal crust had only 27 to 56% of the TLB of plants grown without algal crust (Fig 5.10). Over the entire study period of 26 days, only the plants grown without crust in sites A and B produced an average of more than one leaf; other plants produced less than half a leaf on average over the study period. It was also only the plants grown without crust in sites A and B that produced axillary shoots. For both sites, an average of 10% of leaf births were on axillary shoots (total leaf births are therefore not distinguished into main and axillary shoot components).

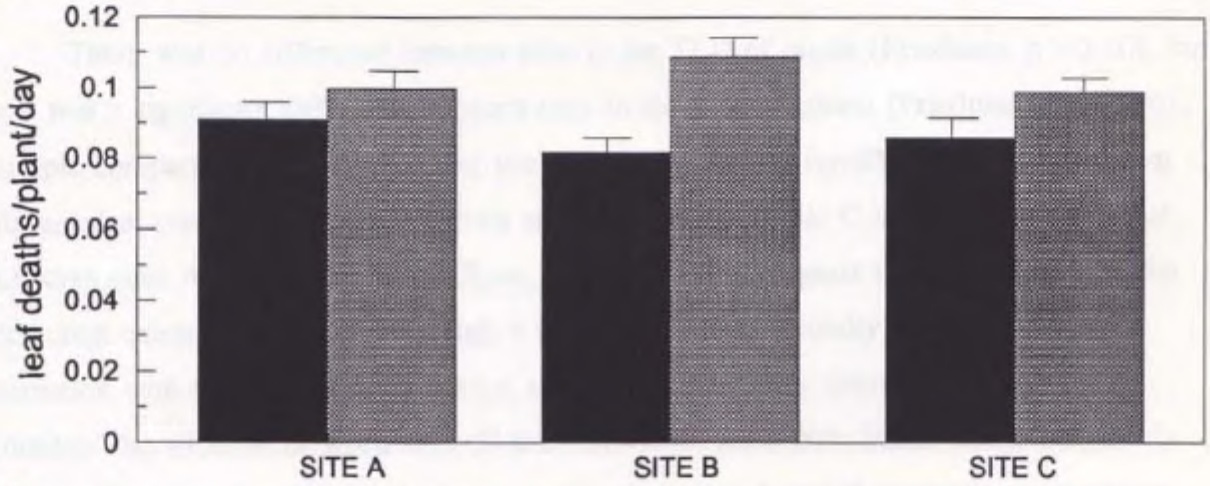
The total leaf death rate (TLD) was significantly higher for plants grown in the intact algal crust (Friedman test, $p<0.001$; Fig 5.10). Plants grown without an algal crust had 74 to 91% of the TLD of plants grown in the algal crust. All leaf deaths were on main shoots.

Fig 5.10. Total leaf birth rates (a), death rates (b) and plant mortality (c) of *Puccinellia* plants grown with or without algal crust in three sites. Bars in (a) and (b) represent mean values for 25 plants, and error bars are $\pm$ 1 SE.

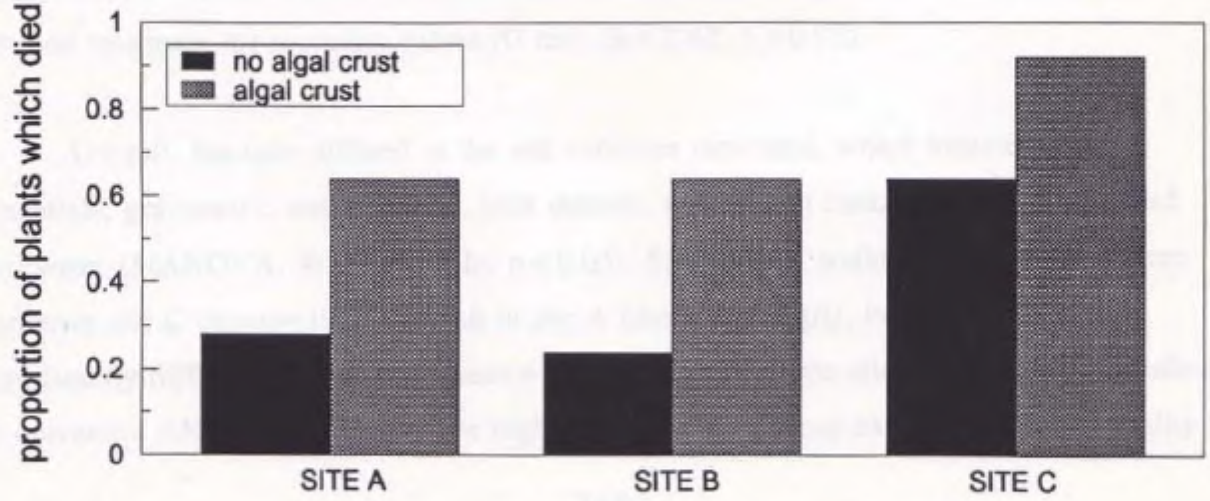
a


leaf births/shoot/day
0.06
0.05
0.04
0.03
0.02
0.01
0
no algal crust
algal crust
SITE A
SITE B
SITE C

b


leaf deaths/plant/day
0.12
0.1
0.08
0.06
0.04
0.02
0
SITE A
SITE B
SITE C

c


proportion of plants which died
1
0.8
0.6
0.4
0.2
0
no algal crust
algal crust
SITE A
SITE B
SITE C

Leaf death rates exceeded leaf birth rates on all sites and in both treatments, indicating that no plants were accumulating leaves. Both the TLB and TLD of plants were a fraction (less than 25%) of those recorded in high biomass sites in 1983 (Bazely, 1984) and 1991 (this Chapter).

By the end of the study period, leaf death rates had exceeded leaf birth rates to such an extent that in some plants that no living leaves remained on the plant, and the plant was declared dead. Significantly more plants died among those grown with algal crust than those grown without an algal crust (G test, $G_3=21.2$, $p<0.005$). Mortality varied from 64 to 92% for plants grown with an algal crust, and from 24 to 64% for plants grown without the algal crust (Fig 5.10).

There was no difference between sites in the TLD of plants (Friedman, $p>0.10$), but there was a significant difference between sites in the TLB of plants (Friedman, $p<0.001$). Multiple comparison tests indicate that site differences are not significant for plants grown with an algal crust, but for plants grown without algal crust, site C has significantly lower TLB than sites A and B (Joint Rank Ryan, $p<0.05$). This suggests that a treatment by site interaction exists for TLB, even though it is not possible to formally test for such an interaction with this experimental design, unless the underlying distribution is known. Mortality also differed between sites (G test, $G_4=18.9$, $p<0.005$; Sokal and Rohlf, 1981), with site C having significantly higher mortality than sites A and B (multiple comparisons with G test, $\alpha=0.05$; Sokal and Rohlf, 1981). There was no significant association between site and treatment for mortality values (G test, $G_2=2.42$, $p>0.05$).

Overall, the sites differed in the soil variables measured, which included redox potentials, gravimetric water content, bulk density, and sodium concentrations in extracted soil water (MANOVA, Wilks Lambda, $p<0.05$). Specifically, sodium concentrations were higher in site C (mean=19.1 g/l) than in site A (mean=11.8 g/l), but neither site was significantly different from site B (mean=16.4 g/l; Tukey's tests after a significant site effect in univariate ANOVA, $p<0.05$). The high salinity of site C may explain the high mortality

of plants in this site, compared to sites A and B. A site effect was not significant for the other soil variables. There was no overall effect of either treatment, or a site by treatment interaction (MANOVA, Wilks Lambda, $p > 0.05$).

5.6 **Discussion**

Leaf birth and death rates were often positively correlated in this study. In part this is because leaf death rates are limited by the supply of new live leaves. In dying and slowly growing plants, leaf death rates may be low because there are no or only a few living leaves. In vigorously growing plants, leaf birth rates and death rates are often both high, signifying a high leaf turnover rate (Chapter 6).

On average, *Puccinellia* plants did not grow more vigorously in low biomass sites compared to high biomass sites in either 1991 or 1992. In 1991, plants produced and lost the same number of leaves over the study period in high and low biomass sites. In 1992, plants produced and lost significantly more leaves in high biomass sites compared to low biomass sites (and more in low biomass sites compared to bare sites). Plant mortality was lower in high biomass sites than in low biomass sites in both years, but was higher in general in 1992. These differences in results between years are probably largely due to differences in weather conditions. Air temperatures in June, July and August were much warmer in 1991 than in 1992, especially for the two weeks after transplanting (see Fig 1.4). Despite the warmer temperatures in 1991, soils did not appear to be more saline (Fig 4.3), probably because of more precipitation over the study period in 1991 (Fig 1.4). Overall, the study period in 1991 was warmer and wetter than average, and the study period in 1992 was colder and drier than average (Fig 1.4: Chapter 1).

In both years, both soil salinity and plant growth were more variable in low biomass sites than in high biomass sites. In both years, much of this variation in plant growth in low biomass sites could be explained by a decrease in production and loss of leaves with increasing soil salinity. Plants in low biomass sites with below-average soil salinity actually

produced as many or more leaves than those in high biomass sites. Such low biomass sites may eventually be converted into high biomass sites, as evidenced by biomass increases in low biomass sites 5 and 6 (1992). Plants in other low biomass sites with above-average soil salinity in 1991, and with average soil salinity in 1992, had much poorer rates of leaf production and shoot survivorship than those in high biomass sites, and such low biomass sites may be in the process of being converted to bare areas.

High biomass, low biomass, and bare areas differ both in plant density (biomass) and soil salinity. In both years, demography of main shoot leaves appeared to be dependent largely on differences in soil salinity between sites, while axillary shoot demography appeared to be dependent on differences in both density (biomass) and soil salinty. These generalizations are true not just for differences between biomass categories, but also for the smaller variation in plant density and soil salinity in low biomass sites in 1991. An increase in soil salinity decreased rates of leaf production and loss on main and axillary shoots, while an increase in density increased leaf production and loss on axillary shoots. The latter may be interpreted as a crowding effect: as intraspecific competition for nutrients and space increases as plant density increases, plants will tend to devote less resources to lateral expansion (White, 1985; Watkinson, 1985). Similar effects of conspecific density on the production of lateral branches have been demonstrated for *Salicornia europaea* (Ellison, 1987a). Since low biomass sites have lower plant densities and greater soil salinity than high biomass sites, axillary shoots in these sites will experience tendencies to produce, respectively, both more and fewer leaves than in high biomass areas. In 1991, these two tendencies equalled each other, on average: plants in low and high biomass sites had similar rates of ASLB and ASLD. In low biomass sites of below average salinity, the effects of density dominated: production of axillary shoots and axillary shoot leaves exceeded that of plants in high biomass sites. In low biomass sites of greater than average salinity, the effects of salinity dominated: production of axillary shoots and axillary shoot leaves was less than that of plants in high biomass sites. Similar interactions between intraspecific competition and salinity have been reported by Badger and Ungar (1991).

Both axillary shoot and main shoot leaf production decreased with increasing salinity. The reduction of ASLB was proportionately greater. For example, for plants in low biomass sites in 1991, the slope of the regression equation between ASLB (leaves/plant/day) and sodium concentration (g/l soil water; explanatory variable) was -0.0219, but was only -0.00610 for MSLB (Fig 5.7; slopes do not include the effect of density). Consequently, the ratio of ASLB:MSLB decreases from 1.21 in low biomass sites of low salinity (0 to 2 g/l Na) to 0.69 in low biomass sites of high salinity (4 to 8 g/l Na) in 1991. Low biomass sites of average salinity in 1992 produced no axillary shoots so similar comparisons cannot be made for this year. Salinity has been reported previously to affect resource allocation between shoots and roots (eg., Parrondo et al., 1978; Osmond, 1980; Munns and Termaat, 1986) and between reproductive and vegetative structures (Jefferies, 1972; Kingsbury et al., 1976; Gray and Scott, 1977; Jefferies et al., 1979b; Jerling and Liljelund, 1984; Badger and Ungar, 1991), although both effects vary between species (reviewed in Adam, 1990). In *Puccinellia*, axillary shoots may serve various functions, including the avoidance of grazing (Bazely and Jefferies, 1989), replacement of the main shoot after its grazing-related death (pers. obs.), conversion of the plant from a phalanx to a guerrilla growth form (Lovett Doust, 1981; Schmid and Harper, 1985), and acting as vegetative propagules for dispersal (Chou et al., 1992) and colonization (Jefferies, 1988b). These may be non-essential and costly functions for plants experiencing stress from high soil salinities. The comparatively larger main shoots may be favoured under these conditions.

Plant demography was not examined in bare areas in 1991. Based on the above discussion, differences in plant demography between low biomass and bare areas in 1991 would have been influenced both by changes in plant density and salinity. The positive effects of lower plant density in bare areas on axillary shoot production might be predicted to be minor, since plants are already 1.2 cm apart in low biomass sites. The deleterious effects of salinity are predicted to be proportionally greater at higher salinities: for example the negative quadratic function between salinity and ASLB (and hence TLB: Table 5.3) indicates that salinity has little effect at low levels, but a much greater effect at high levels. A similar effect is evident for MSLB (Fig 5.7). The net effect of these two trends could have been

lower rates of main and axillary shoot leaf production in bare areas, relative to that in low and high biomass sites, in 1991. Certainly in 1992, total leaf birth rates were lower for plants in bare areas relative to those in low and high biomass areas.

The presence of algal crusts reduced shoot survival and total leaf births and deaths in bare areas. Similar dry and tough algal crusts are also found in low biomass sites, but not in high biomass sites (the soil surface is much more moist). It is unlikely, however, that the presence of algal crusts is entirely responsible for lower plant growth in low and bare sites compared to high biomass sites. If so, differences in demography of plants between low biomass and bare sites (1992) and within low biomass sites (1991) would be minor (since all sites have algal crust) and would not be explained by variation in soil salinity (soil salinity was not correlated with algal crust presence in 1992: section 5.5.9).

Algal crusts (ie., dry algal mats) are common in many salt marshes (Golubić, 1973; Adams, 1990), and thick dried algal crusts have been noted in non-tidal saline areas (Ehrlich and Dor, 1985). Blistering algal crusts, similar to those at La Pérouse Bay, are formed on well-drained sediments with prolonged exposure to drying conditions (Golubić, 1973). Under these conditions, high rates of anaerobic decomposition occur and the consequent accumulation of CO_2 under the algal crust causes blistering (Golubić, 1973). This mechanical lifting of the drying algal crust could have abraded or exposed roots of *Puccinellia* grown in algal crust. Algal and other soil crusts are reported to reduce water infiltration and hence can cause high surface salinities (Golubić, 1973; Price et al., 1989; Graetz, 1991). It is possible that algal crusts reduced water infiltration to *Puccinellia* roots and/or increased soil salinity, but the presence of algal crusts did not appear to significantly affect either soil water content or soil salinity. Lastly, algal crusts could have reduced *Puccinellia* growth by direct toxicological effects. Algae have been reported to inhibit vascular plant growth in salt marshes, but only in wet, filamentous mats which cover or otherwise reduce irradiance to plants (Ranwell, 1981, in Adam, 1990; Jensen and Jefferies, 1984). Clearly, this is not the case for dry algal crusts.

The effects of grazing and plant origin on leaf demography are complex and not consistent between demographic variables. In 1991, grazing tended to increase axillary shoot leaf birth and death rates, but this effect was complicated by a grazing by origin interaction (section 5.5.4.1). In this year, grazing also tended to decrease main shoot leaf births in less saline sites, but had little effect in more saline sites (sections 5.5.4.1, 5.5.7.1). This could indicate that when soils become saline enough, salinity stress can overwhelm grazing stress, but it could also just reflect lower grazing pressure in the more saline sites (Fig. 5.8). In 1992, grazing significantly reduced total leaf deaths but not births in all sites (section 5.5.4.2, 5.5.7.2). Perhaps the only overall conclusion that can be made from these analyses is that the effects of grazing and origin are consistently only just significant or non-significant, in contrast to the effects of biomass or soil salinity which are highly significant. This is conclusion was also evident from the results of the MANOVA analysis.

It should be noted that "grazing" includes a variety of effects on leaf production including the possible loss of leaves to herbivory (negative effect: Sadul, 1987; Hik et al, 1991), conversion of plant biomass into faeces (positive effect: Bazely and Jefferies, 1985, 1985; Reuss et al., 1989), creation of small patches which are colonized by cyanobacteria (positive effect: Bazely and Jefferies, 1985), and trampling (negative effect: Hik and Jefferies, 1990). Between 1979 and 1986, at least, net above-ground primary production (NAPP, measured in g/m^2) of high biomass *Puccinellia* swards at La Pérouse Bay was increased by these combined effects of grazing (Cargill and Jefferies, 1984a; Bazely, 1984; Hik and Jefferies, 1990; Hik et al., 1991).

In 1983, leaf and shoot demography of *Puccinellia* was examined in grazed and ungrazed high biomass swards in La Pérouse Bay (Bazely and Jefferies, 1989). In grazed swards, relative to ungrazed swards, leaf birth rates were lower for main shoots (MSLB) but greater for axillary shoots (ASLB), with the sum (TLB) being greater for plants in grazed swards. The immediate cause of the enhancement of NAPP by grazing in 1983 was therefore greater ASLB (which included greater production of axillary shoots) in grazed areas. Comparison of seasonal demographic data from 1983 and that from 1991 and 1992 (this

Table 5.4. Leaf demography (based on leaf change over the season; see text for abbreviations) of *Puccinellia phryganodes* in grazed and ungrazed areas in high biomass swards. All plants originated from high biomass sites; plants were not disturbed in 1983, but transplanted in 1991 and 1992. Data from 1983 are calculated from Fig. 1 in Bazely and Jefferies (1989), and 1991 and 1992 values are from this study. All data are in rates (leaves/plant/day).

	Grazed Plots			Ungrazed Plots		
	1983	1991	1992	1983	1991	1992
MSLB	0.064	0.094	0.089	0.092	0.101	0.089
MSLD	0.092	0.103	0.103	0.092	0.105	0.110
ASLB	0.118	0.020	0.007	0.077	0.050	0.006
ASLD	0.068	0.011	0.001	0.022	0.030	0.001
TLB	0.182	0.114	0.096	0.169	0.152	0.095
TLD	0.160	0.113	0.104	0.114	0.135	0.111

study) indicates that while grazed areas had higher TLB in 1983, this was not true in 1991 or 1992 (data for plants of high biomass origin growing in high biomass sites is used for 1991 and 1992, to make the comparison consistent between years: Table 5.4). In fact, TLB tended to be higher in exclosed areas than in grazed areas in 1991. Leaf demography is very similar in exclosed areas in both 1983 and 1991, but differs dramatically in grazed areas. Specifically, in grazed areas MSLB is somewhat higher in 1991, but ASLB is an order of magnitude lower in 1991, with the result that the TLB in 1991 is only 63% that of 1983. In 1992, main shoot demography is similar to that of 1983 and 1991 in exclosed areas, and to that of 1991 in grazed areas, but in all areas ASLB is much lower than that of either 1983 or 1991; this presumably reflects the adverse growing conditions of 1992 discussed earlier.

It could be argued that these comparisons are confounded by differences in methodology between years. In 1983, plants were not disturbed, while in 1991 and 1992 transplanted plants were used. The similarity in demography in exclosed areas in all years (save axillary shoot demography in 1992), however, argues against transplanting having a large effect. In 1983, only one of four demography plots was in the eastern salt marsh of La Pérouse Bay, while all plots in 1991 and 1992 were in this region. Although significant site differences existed for axillary shoot production in 1983, the site in the eastern salt marsh produced a similar number of axillary shoots (1.81 shoots/plant/67 days) as the average (1.89 shoots/plant/67 days). In 1983, demography was examined over 67 days, while demography was examined over 57 and 33 days in 1991 and 1992 days respectively. Although axillary shoot production tends to be slow early in the season (Fig. 1: Bazely and Jefferies, 1989; pers. obs.), differences between grazed and exclosed areas in both ASLB and MSLB were evident by the first 33 days of the study 1983. Otherwise, details of the methodology was remarkably similar: several sites with adjacent grazed and exclosed areas were examined in all years, temporary exclosures of 0.75m x 0.75m were used in 1983 and of 1m x 1m were used in 1991 and 1992, and demographic recording techniques and analyses were identical between years.

It appears, therefore, that plant demography in grazed high biomass swards is not the

same between the early 1980's and the early 1990's. Above-ground biomass of grazed high biomass swards appears to have decreased over this period (Williams et al., 1993), but it is not clear if this is due to a reduction in plant size, a reduction in plant density, or both. The scarcity of axillary shoots in such areas in 1991 suggests a reduction in plant size, at least laterally (lack of axillary shoots in grazed areas in 1992 is confounded by lack of axillary shoots in exclosed areas and is not discussed).

There are several possible reasons for fewer axillary shoots in 1991. The intensity of grazing may differ between 1983 and 1991. If production of axillary shoots is a strategy to avoid clipping of leaves by geese (leaves are less likely to be grazed on axillary shoots than on main shoots: this chapter), then the ratio of resources put into axillary shoots versus main shoots (ie, ASLB: MSLB) should be greater in years with high grazing pressure. Such a shift in strategy is suggested by higher ASLB in 1983 compared to 1991, but higher MSLB in 1991 compared to 1983. At present, differences in grazing pressure between 1983 and 1991 are not known (R.L. Jefferies, pers. comm.). If above-ground biomass is lower in 1991 than 1983, then such biomass-related edaphic conditions as soil salinity and moisture content may be less favourable in 1991 even in high biomass sites. For example, soil salinity decreased in high biomass areas after just two weeks of exclosure in 1992 (Fig. 5.4; see also Bazely, 1984). Results discussed earlier and in Chapter 6 indicate that *Puccinellia* responds to higher soil salinity primarily by switching (dimishing) resources from axillary shoots into main shoot leaves. The low axillary shoot production in 1991 is therefore also consistent with a higher soil salinity in 1991 compared to 1983. Lastly, if plants are smaller in 1991 than in 1983, axillary shoot production may be constrained by plant size (since only one axillary shoot can occur in each leaf axil).

5.7 **Implications for the positive feedback hypothesis**

The results suggest that on very warm and wet summers, like that of 1991, *Puccinellia* growth is not related to biomass (although bare areas were not examined: plant growth might well have been low in such areas), but on cold and dry summers, like that of

1992, *Puccinellia* growth and survival is positively correlated to biomass (through the effects of salinity and algal crusts). Furthermore, *Carex* survivorship was greater in high biomass areas than in bare areas, at least in 1992 (although it could not be determined which graminoid was most affected by biomass differences).

Leaf demography and plant mortality are not the only determinants of biomass change in an area. Also important are rates of vegetative propagule entry or production, and establishment of these propagules. These were not examined in this study, but it is expected that establishment will be severely restricted by (dry) algal crusts and salinity in low biomass and bare areas.

Lastly, the role of soil salinity in reducing leaf production and plant survivorship should be interpreted with caution. Many other possibly important site variables were not examined, such as nitrogen inputs and availability, other macro- and micro-nutrients and their ratios, organic matter content, and possible interactions with other organisms such as nematodes and mycorrhizae. Soil salinity may have been more strongly correlated with plant performance than soil moisture content or soil oxidation simply because differences in soil salinity tend to accumulate (Chapter 4), while soil moisture and redox potential return to saturated and reduced conditions, respectively, after each rainfall event.

CHAPTER 6: EFFECT OF SALINITY ON THE GROWTH OF GRAMINOIDS PLANTED IN POTS

6.1 Introduction

Most salt-marsh plants have maximal growth under non-saline conditions (Adam, 1990; Ungar, 1991). Growth has most often been measured as change in biomass (dry weight) after a period of treatment, although sequential harvests have been used to calculate relative growth rates for each interval during the duration of the experiment (eg., Jensen, 1985; Shennan et al., 1987). A refinement of these techniques is the measurement of leaf elongation or area, which allows repeated measurements of the same plant. In both cases, however, only the difference between production and death of either leaves or biomass is measured. Jefferies and Rudmik (1991) have argued that measurements of biomass give little information on the growth of plants in a saline environment, in contrast to demographic techniques which provide information on both the production and loss of leaves, as well as the difference between leaf production and loss. Munns and Termaat (1986) suggest that plant mortality in high salinity is caused by an asymmetry between leaf production (including expansion) rate and leaf death rate. Once leaf death rate exceeds leaf production rate, photosynthetic area decreases, causing a reduction in carbohydrate reserves, which further reduces leaf production until the plant dies. Both plant growth and mortality in saline conditions are therefore best understood in terms of leaf or biomass production and loss, rather than their difference.

In this study, demographic techniques were used to measure the effect of salinity on leaf birth and death rates of *Puccinellia phryganodes* and *Carex subspathacea*. Soil salinity has been postulated to have a major influence on both *Puccinellia* and *Carex* leaf demography and survivorship of plants in the field (Chapter 5). Soil salinity has also been suggested to cause small-scale differences in distribution between these two species (Mason, 1981). Other factors correlated with salinity in the field, such as soil moisture, could, however, be more important. The effect of salinity is isolated by examining the response of

these two graminoids to salinity in controlled experiments with potted plants. Salinity conditions in pots only approximate to those in the field, even when potted plants are grown under field conditions, because of the different water status of the soil. However, the trend in phenotypic response to increased salinity is anticipated to be similar in both pots and the field. The objectives of this experiment were 1) to compare the salt tolerance of *Puccinellia* and *Carex*, 2) to examine *Puccinellia* growth over both small and large ranges of salinity in pots in the field and in growth chambers, and 3) to compare growth in pots under field conditions to growth of transplanted plants in the La Pérouse Bay salt marsh in the same years (similarities are predicted by positive feedback hypothesis 5, Chapter 1).

6.2 Methods

6.2.1. Demography of *Puccinellia phryganodes* and *Carex subspathacea* plants grown under field conditions (1991)

In late June, 1991, turves containing *Puccinellia* and *Carex* plants were collected from a small area (c. $1m^2$) of sward in the salt marsh at La Pérouse Bay. Care was taken to obtain plants from a small area, as previous studies have indicated considerable genetic variability even within an area of 50m x 50m at La Pérouse Bay (Sadul, 1987). Shoots of *Puccinellia* and *Carex*, of similar size and with a well developed root system, were carefully removed from the turves (n=100/species), and were individually planted in pots (7 cm maximum diameter) containing a peat-silt-sand mixture obtained from La Pérouse Bay. Potted plants of both species were randomly assigned to five salinity treatments (20 plants/ species/ treatment), and randomly positioned in a 1m x 2m area just inland from the salt marsh (at the Queen's University Tundra Biome Research Station). Plants were grown outside, and were completely exposed to natural conditions (including rainfall events).

Plants were watered daily (10 ml water/pot). For the week after transplanting, plants were watered only with non-saline water to minimize transplant shock. The salinity of the watering solution was then increased by 8 g dissolved salts/l every day in the appropriate

pots until pots were watered with solution of either 0, 8, 16, 24, or 40 g dissolved salts/l. Saline solutions were made using "Instant Ocean" aquarium salt (Aquarium Systems, Mentor, Ohio). The composition of aquarium salts approximates the composition of saline water experienced by salt-marsh vegetation (especially intertidal salt-marsh vegetation). Numerous studies have shown that growth is affected by the ratio of individual salts, not just the total osmotic potential (Osterhoult, 1906, in Gale, 1975a; Lagerwerff and Eagle, 1961; Munns and Termaat, 1986). Salinity of the watering solutions was measured using a portable salinity meter (Yellow Springs Instrument Co. Inc., Ohio, U.S.A., model 33). Pots were flushed at least once a week by rainfall or by watering with freshwater to prevent excessive salt accumulation.

Plant demography was assessed on five census dates 13-14 days apart: July 4, July 17, July 31, and August 13, 1991. Watering with saline water began immediately after the first demography census. The first interval, therefore, included a few days of growth at a low salinity (when the salinity of the watering solution was being increased), but these 0 to 5 days probably have little effect on overall results. Details of demographic techniques and parameters are given in Chapter 2; only seasonal demographic parameters were calculated.

One *Carex* plant was destroyed (by a gosling) during the study, so the *Carex* demography was analyzed by a general linear model approximation of ANOVA and MANOVA (type III sum of squares). Equal sample sizes existed for *Puccinellia*, so conventional ANOVA and MANOVA analyses were performed. Some data had to be transformed to reduce heteroscedasticity (Bartlett's test, $p<0.05$). Specifically TLB (abbreviations defined in results section) and TLD of *Puccinellia* and ASLB and ASLD of *Carex* were log-transformed (after the addition of 0.01 to avoid values of 0), and the square root was taken of ASLB of *Puccinellia* and TLB of *Carex*. Most of these transformations were necessary because variances were positively correlated with the mean of particular demographic parameters. For the ASLD data of *Puccinellia*, however, variances were low in one of the treatments with a high mean, so standard transformations could not reduce the heteroscedasticity. These data were analyzed using a Kruskal-Wallis test (Chi-squared

approximation; Sokal and Rohlf, 1981) and were excluded from the MANOVA analyses. All statistical analyses were performed using SAS software (SAS, 1988).

6.2.2 Demography of *Puccinellia phryganodes* plants grown in pots under field conditions (1992)

In early July, 1992, individual *Puccinellia* shoots were isolated from a 0.5m x 0.5 m area of salt marsh immediately adjacent to the area from which plants were removed for demography in 1991. Plants were planted in pots, randomly assigned to five salinity treatment categories (n=31/treatment) and positioned outside, as described above.

Plants were watered daily (10 ml water/pot). Plants were watered with non-saline water for two days after transplanting, and then with gradually more saline water over the next six days, as appropriate, until plants were watered with solution of either 0, 20, 40, 60, or 80 g dissolved salts/l. Saline solutions were made from aquarium salt as described earlier.

Plant demography was assessed on three census dates 13 days apart: July 12, July 25, August 7. The first demographic census, on July 12, was immediately after the salinity of the watering solution had reached its final concentration.

In extreme treatments, there were no leaf births and almost all existing leaves died, causing low variances and non-normal distributions (Bartlett's and Shapiro-Wilks tests, respectively; SAS, 1988). Data was therefore analyzed by the use of Kruskal-Wallis tests (Sokal and Rohlf, 1981), followed by Steel-Dwass rank tests for multiple comparisons (Miller, 1966). The Steel-Dwass rank test was the most powerful simultaneous non-parametric test for unplanned multiple comparisons examined by Day and Quinn (1989), and controls the experimentwise error rate. It is not possible to examine overall effects with MANOVA, because of the non-parametric nature of the data.

6.2.3. Demography of *Puccinellia phryganodes* plants grown in pots in a growth chamber.

In late August, 1991, a 20 cm x 20 cm x 10 cm turf was removed from a *Puccinellia-Carex* sward in the salt marsh (adjacent to areas from which plants were removed for the demography experiments described above). The turf was transported to the University of Toronto. From the turf, 105 *Puccinellia* plants were isolated and planted individually in pots (6 cm maximum diameter, 5.5 cm height) in a peaty soil mixture. Plants were randomly divided into seven salinity treatments: 0, 20, 30, 40, 50, 60, and 70 g dissolved salts/l. Pots of the same treatment were suspended by a frame in a tray of solution of the appropriate salinity. The saline solution covered the bottom 1.5 to 2 cm of the pots.

Salinity of the culture solutions was increased gradually, as described in Table 6.1. Again, saline solution was made with aquarium salts, and salinity measured with a salinity meter. The water was changed two to three times a week, and the trays scrubbed weekly to remove any algae. All plants were grown in a growth chamber, at 15 °C, with a 12-hr dark period and 12-hr light period (photon flux density c. 200 μmoles m^{-2} s^{-1}). Tray position within the growth chamber was randomized twice a week.

Plant demography was assessed on 9 weekly censuses from October 18 to December 20, 1991, except on Dec 13, 1991 (Table 6.1). Demographic data was analyzed for the last four weeks of the experiment, when all plants had had at least a week to adjust to the final salinity. All plants showed similar leaf birth and death rates in the first three weeks, before any salts were added (results not shown).

Data was non-normal and variances unequal for reasons mentioned above. Kruskal-Wallis and Steel-Dwass rank tests were therefore used, as above.

Table 6.1. Salinity of the culture solutions after the water was changed, and demography census dates. *Puccinellia phryganodes* plants were grown in a growth chamber in pots which were partially immersed in the culture solutions. Leaf demography was examined by a weekly census (Y) but not every time the culture solution was changed (N).

		Salinity of culture solutions (g diss. salts/l)						
Day	Census	0	20	30	40	50	60	70
1	Y	0	0	0	0	0	0	0
8	Y	0	0	0	0	0	0	0
15	Y	0	5	5	5	5	5	5
18	N	0	10	10	10	10	10	10
20	N	0	15	15	15	15	15	15
22	Y	0	20	20	20	20	20	20
25	N	0	20	25	25	25	25	25
27	N	0	20	30	30	30	30	30
29	Y	0	20	30	40	40	40	40
32	N	0	20	30	40	50	50	50
34	N	0	20	30	40	50	60	60
36	Y	0	20	30	40	50	60	70
39	N	0	20	30	40	50	60	70
41	N	0	20	30	40	50	60	70
43	Y	0	20	30	40	50	60	70
50	Y	0	20	30	40	50	60	70
57	N	0	20	30	40	50	60	70
64	Y	0	20	30	40	50	60	70

6.3. RESULTS

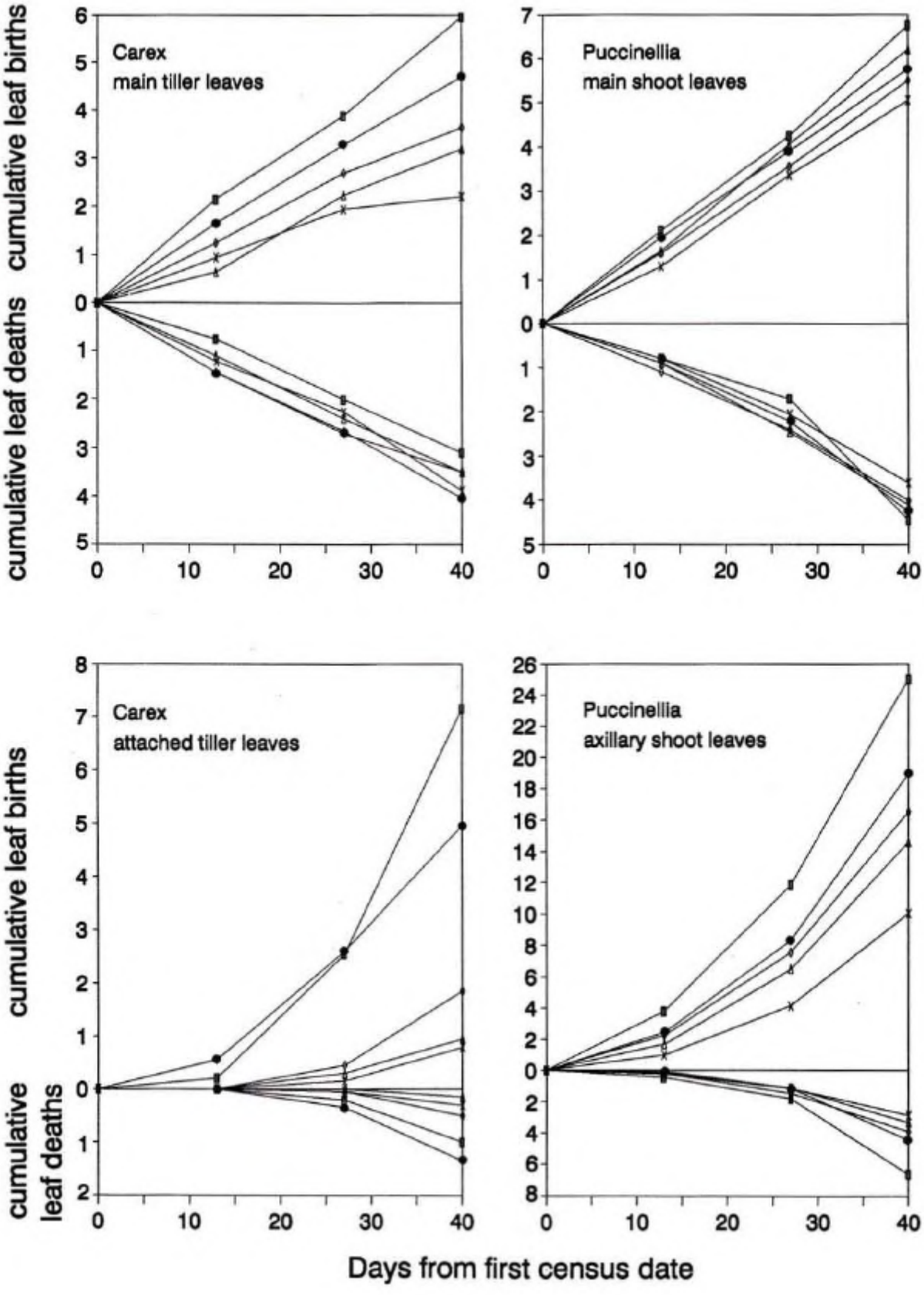
6.3.1. Demography of *Puccinellia phryganodes* and *Carex subspathacea* grown in pots under field conditions (1991)

Over the 40 day study period, rates of leaf births and deaths were uniform within each salinity treatment for both *Carex* and *Puccinellia* (Fig. 6.1). Cumulative values of leaf birth and death rates over the entire study period are used in the statistical analyses given below.

Overall, there was a highly significant effect of salinity on *Carex* leaf demography (MANOVA, Wilk's Lambda, $p<0.0001$). Specifically, there was a significant effect of salinity on main tiller leaf birth rates (MTLB), attached tiller leaf birth and death rates (ATLB and ATLD), and total (main and attached tiller) leaf birth and death rates (TLB and TLD; univariate ANOVAs, $p<0.0005$). Main tiller leaf death rate (MTLD) was not significantly affected by salinity (ANOVA, $p>0.05$). Plants watered with either 0 or 8 g dissolved salts/l had a significantly higher MTLB than those watered with either 24 or 40 g dissolved salts/l, and a significantly higher ATLB and TLB that those watered with either 16, 24 or 40 g dissolved salts/l (Tukey's tests, $p<0.05$). Plants watered with 8 g dissolved salts/l had significantly higher ATLD and TLD than those watered with 24 g dissolved salts/l (Tukey's tests, $p<0.05$). All other comparisons are not significant. The ratio of ATLB to MTLB was 1.20, 1.05, 0.51, 0.30 and 0.36 for plants watered with 0, 8, 16, 24 and 40 g dissolved salts/l respectively: plants appear to preferentially allocate resources to growth of main tillers, not attached tillers, when exposed to high salinities.

Overall, salinity did not affect the leaf demography of *Puccinellia* (MANOVA, Wilk's Lambda, $p>0.05$; ASLD data non-parametric, so analyzed separately). Although overall effects are of primary interest, the specific effects were also examined to determine what, if any, differences existed between them. Neither main shoot leaf birth or death rates (MSLB, MSLD) were significantly affected by salinity (ANOVAs, $p>0.05$), nor axillary shoot death

Fig. 6.1. Cumulative leaf birth and death rates on *Puccinellia phryganodes* and *Carex subspathacea* plants grown in pots under natural conditions at La Pérouse Bay in 1991. Plants were watered with either 0 (□), 8 (●), 16 (◇), 24 (△), or 40 (X) g dissolved salts/l. Values are means for 19-20 plants.


Carex
main tiller leaves
Puccinellia
main shoot leaves
Carex
attached tiller leaves
Puccinellia
axillary shoot leaves
cumulative leaf births
cumulative leaf deaths
cumulative leaf births
cumulative leaf deaths
Days from first census date

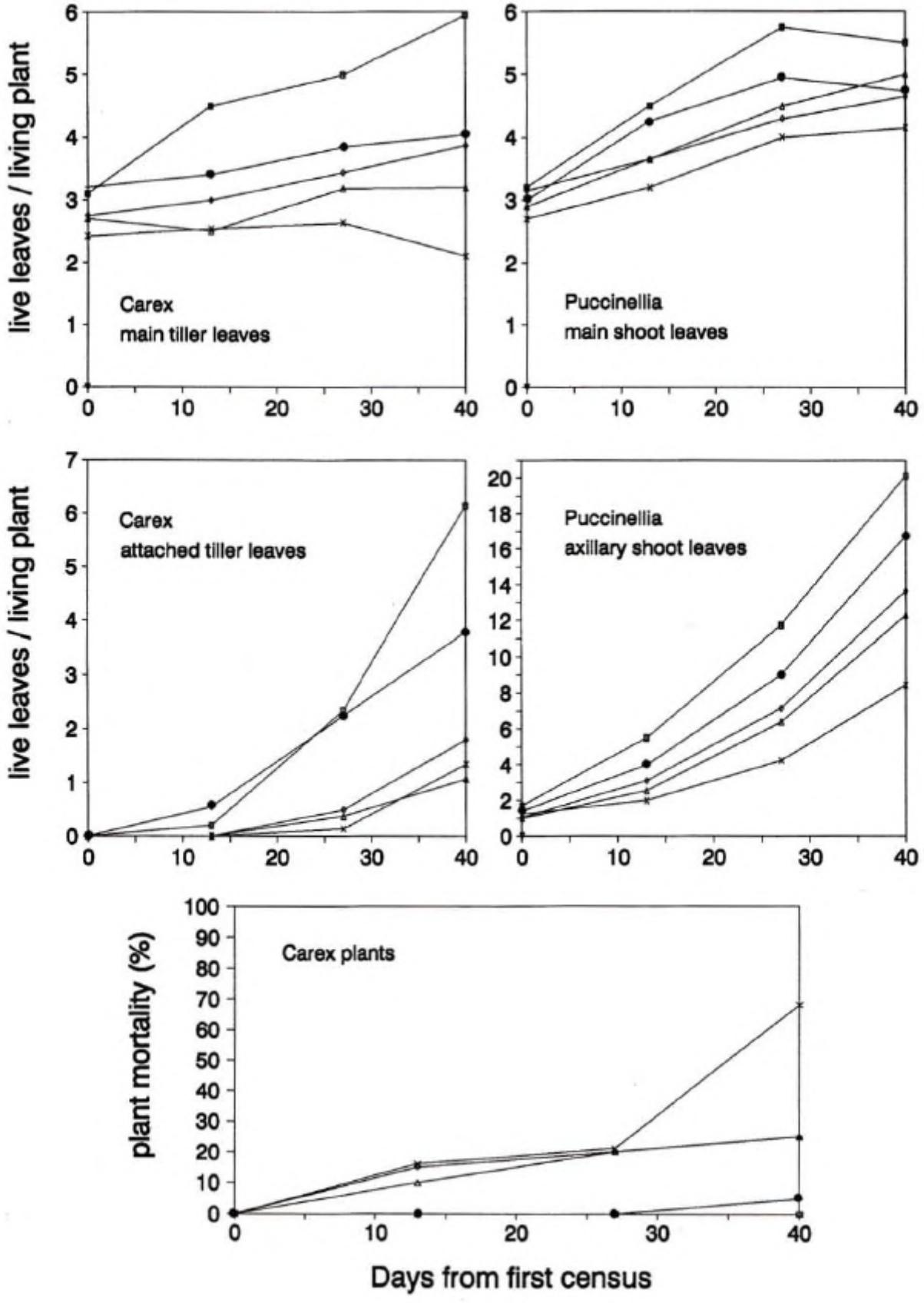
rates (ASLD; Kruskal Wallis test, Chi-squared statistic, $p>0.05$) or TLD (ANOVA, $P>0.05$). By contrast, axillary shoot leaf birth rate (ASLB), and hence TLB, are both significantly affected by salinity (ANOVAs, $p<0.005$). Plants grown at 0 and 8 g dissolved salts/l had a significantly higher ASLB and TLB than plants grown at 16 or 40, but not 24, g dissolved salts/l (Tukey's tests, $p<0.05$). Note that ASLB and TLB are higher at 16 than at 24 g dissolved salts/l when expressed in linear form (Fig 6.1), but when transformed by square-root or logarithms (respectively, to reduce heteroscedasticity) the reverse is true (large value are reduced proportionately more than small values with such transformations, so if only a few large values caused one mean to be greater than the other in linear form, as implied by the original heteroscedasticity, the order of the means can be reversed by such transformations). In any case, plants watered with 16 and 24 g dissolved salts/l had very similar ASLB and TLB. All other comparisons were not significant. As implied by the above results, the ratio of ASLB to MSLB decreased with increasing salinity (3.71, 3.30, 3.00, 2.35, 1.99 for plants watered with 0, 8, 16, 24, 40 g dissolved salts/l respectively). This allocation response to salinity is analogous to that of *Carex*.

Both *Puccinellia* and *Carex* had a reduced TLB when watered with saline solution. It is not legitimate to compare birth rates of these two species directly, since they differ in type of ramet production and leaf size, origin, and structure. However, the percentage decrease of TLB in saline solution (relative to the control, 0 g dissolved salts/l) is greater in *Carex* than *Puccinellia* (Fig 6.2). In *Carex*, MTLB decreased 65% between 0 and 40 g dissolved salts/l, compared to a non-significant decrease of 27% in *Puccinellia* MSLB. Similarly, ATLB decreased by 90% between 0 and 40 g dissolved salts/l in *Carex*, compared to a 59% decrease of ASLB in *Puccinellia*. By the end of the experiment, nearly 70% of all the *Carex* plants grown at 40 g dissolved salts/l had died, while all the *Puccinellia* plants were healthy at this treatment (no plants of either species died at 0 g dissolved salts/l: Fig. 6.3).

Plants exposed to saline solution tended to be of smaller stature with fewer live leaves The reduction in leaf death rates of *Carex* plants with increasing salinity is a result of both fewer live leaves on living plants, and a greater number of dead plants (Fig. 6.3).

Fig. 6.2. Leaf birth rates of *Puccinellia phryganodes* and *Carex subspathecea* plants as a proportion of mean leaf birth rates at 0 g dissolved salts/l. Plants were grown in pots under natural conditions at La Pérouse Bay in 1991 and watered with solution of differing salinity as indicated. Error bars are $\pm$ 1 SE.

Fig. 6.3. Mean number of live leaves per living plant of *Puccinellia phryganodes* and *Carex subspathacea* and mortality of *Carex subspathacea* plants grown under natural conditions at La Pérouse Bay in 1991. Plants were watered with either 0 (□), 8 (●), 16 (◇), 24 (△), or 40 (X) g dissolved salts/l. Values are means for 19-20 plants. Only one *Puccinellia* plant died (= 5% mortality at 8 g dissolved salts/l) so mortality data for *Puccinellia* is not shown. Note that dead plants are not included in the calculation of live leaves per plant.

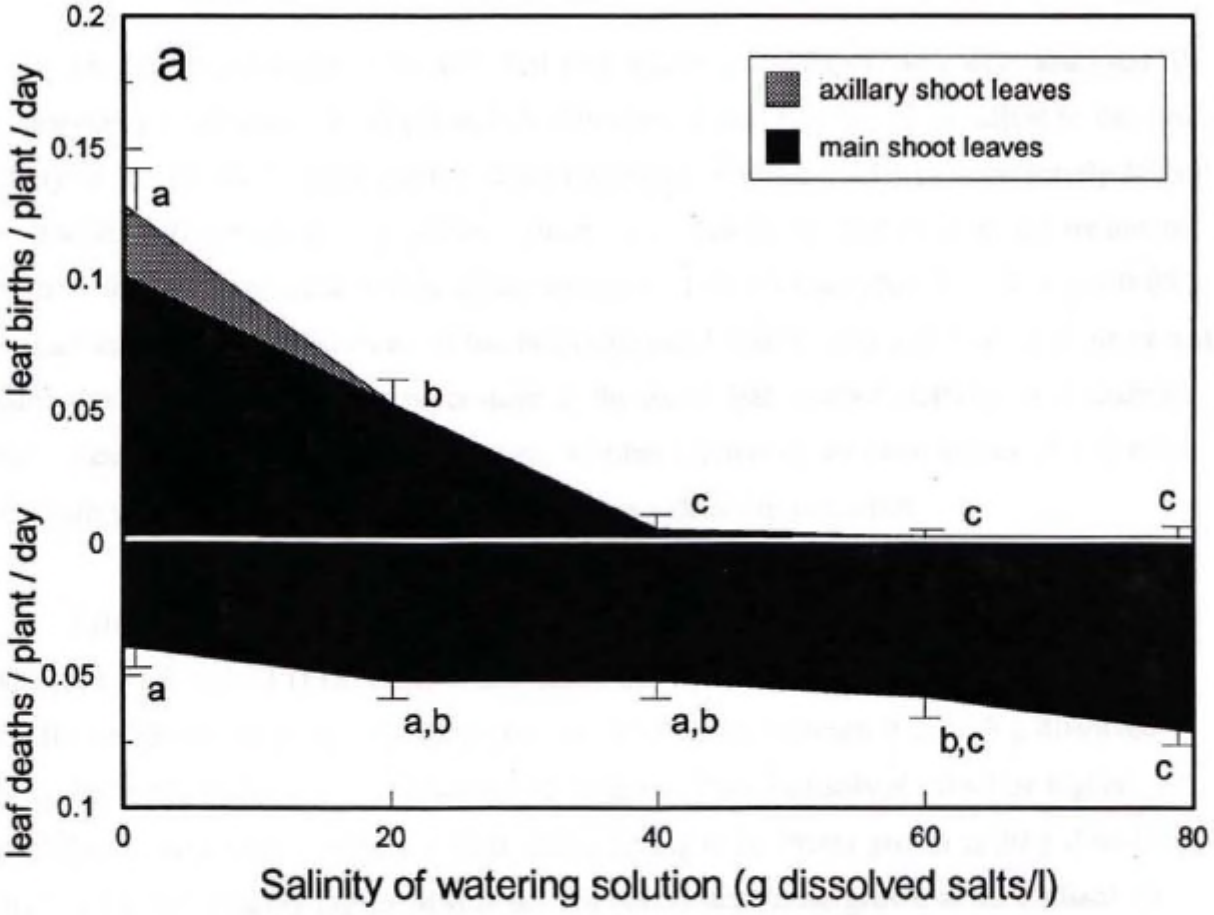

live leaves / living plant
Carex
main tiller leaves
Puccinellia
main shoot leaves
live leaves / living plant
Carex
attached tiller leaves
Puccinellia
axillary shoot leaves
plant mortality (%)
Carex plants
Days from first census

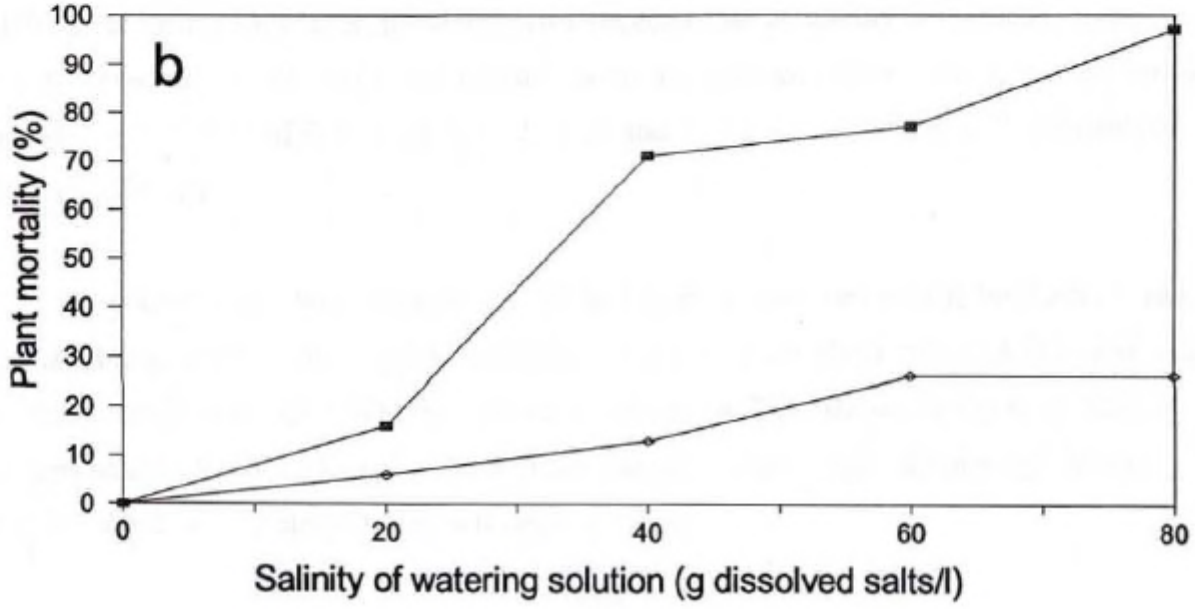
6.3.2. Demography of *Puccinellia phryganodes* plants grown in pots under field conditions (1992)

Both TLB and TLD were significantly affected by salinity (Kruskal-Wallis test, Chi-squared statistic, $p<0.0001$). Significant decreases in TLB occurred between 0 and 20, and between 20 and 40 g dissolved salts/l, but TLB in salinity treatments of, or greater than, 40 g dissolved salts/l was uniformly low (Steel-Dwass rank tests). Differences in TLD between salinity treatments are complex, but generally TLD increases as salinity increases (Steel-Dwass rank tests, results shown in Fig. 6.4). By the end of the experiment, most plants had died in salinity treatments of or greater than 40 g dissolved salts/l (Fig 6.4), as a result of low leaf birth rates and high leaf death rates. Lastly, only plants watered with non-saline solution produced axillary shoots (Fig 6.4).

Puccinellia plants in this experiment came from the same sward and were planted and watered in a similar manner to those in 1991, yet the demography of plants between 0 and 40 g dissolved salts/l were different. Only plants watered with non-saline solution produced axillary shoots in 1992, and the ASLB of these plants was an order of magnitude lower than even those watered at 40 g dissolved salts/l in 1991. There was a clear decrease in MSLB and an increase in TLD between 0 and 40 g dissolved salts/l in 1992, but not in 1991. Plant mortality increased substantially over the same salinity range in 1992 but not 1991. These differences between pot demography in 1991 and 1992 are similar to differences in field demography of transplanted plants in 1991 and 1992 (Chapter 5). Specifically, axillary shoot production, salinity tolerance, and plant survivorship were higher in field demography of plants in 1991 than in 1992. Differences in weather probably account for between year differences in both pot and field demographic data (Fig 1.4).

Fig. 6.4. Leaf birth and death rates (a) and plant mortality (b) of *Puccinellia phryganodes* plants watered with solution of varying salinity. Plant mortality is shown after 13 days (◇) and 26 days (□) of growth, the latter being the end of the experiment. Plants were grown in pots under natural conditions at La Pérouse Bay in 1992. Treatments with the same letter are not significantly different from each other (Steel-Dwass rank tests, $p > 0.05$). Error bars are $\pm$ 1 SE.


a
axillary shoot leaves
main shoot leaves
leaf births / plant / day
leaf deaths / plant / day
0.2
0.15
0.1
0.05
0
0.05
0.1
a
b
c
c
c
a
a,b
a,b
b,c
c
0
20
40
60
80
Salinity of watering solution (g dissolved salts/l)


b
Plant mortality (%)
100
90
80
70
60
50
40
30
20
10
0
0
20
40
60
80
Salinity of watering solution (g dissolved salts/l)

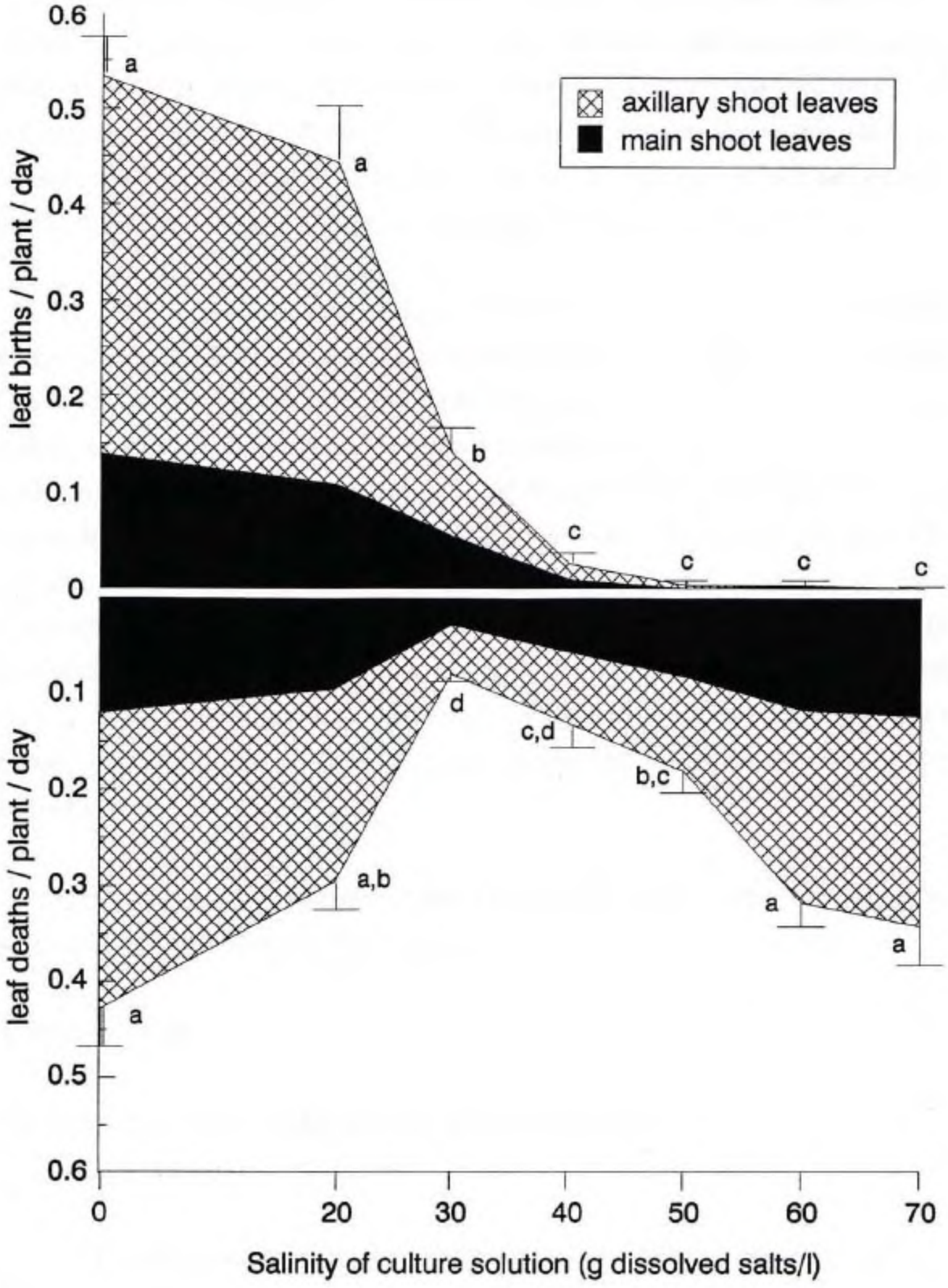
6.3.3. Demography of *Puccinellia phryganodes* plants grown in pots in a growth chamber

Leaf birth and death rates in the last four weeks of the experiment were analyzed. By the beginning of this period, all plants had between one and four weeks to adjust to the final salinity of the solutions. Leaf number at the beginning of this period was significantly higher in 0 and 20 g dissolved salts/l treatments (mean = 15 leaves) than in more saline treatments (mean = 9 leaves), because of this adjustment time (Tukey's tests after ANOVA, $p<0.05$; no other comparisons significant). It has been suggested that in such situations leaf births and deaths should be expressed as a percentage of the initial leaf number (Jefferies and Rudmik, 1991). Results were very similar, however, whether relative or absolute values of leaf birth and death were used; for simplicity, only absolute values are presented.

Salinity had a highly significant effect on *Puccinellia* MSLB, ASLB, MSLD, ASLD, and hence TLB and TLD (Kruskal-Wallis tests, Chi-squared statistic, $p<0.0001$). Both MSLB, ASLB and their sum (TLB) decreased significantly between 0 and 30 g dissolved salts/l, but were uniformly low at salinity treatments of 40 g dissolved salts/l or higher (Steel-Dwass rank tests, results for TLB shown in Fig 6.5). Plants grown at 30 g dissolved salts/l had a significantly higher MSLB but not ASLB than those grown at 40 g dissolved salts/l , and a significantly lower ASLB but not MSLB than those grown at 20 g dissolved salts/l (Steel-Dwass rank tests, $p<0.05$). This suggests that as salinity is increased from 0 to 40 g dissolved salts/l, leaf births on axillary shoots are reduced before main shoot leaf births (the ratio of ASLB to MSLB is 2.82, 3.12, 1.59 and 1.65 for 0, 20, 30 and 40 g dissolved salts/l respectively).

At both low and high salinities ($\leq$ 20 and $\geq$ 60 g dissolved salts/l) both ASLD and TLD are high, while at intermediate salinities (30 and 40 g dissolved salts/l) ASLD and TLD are significantly lower (Steel-Dwass rank tests, results for TLD shown in Fig 6.5). MSLD are significantly lower at 30 g dissolved salts/l than at low and high salinities ($\leq$ 20 and $\geq$ 60 g dissolved salts/l; Steel-Dwass rank tests, $p<0.05$).

Fig. 6.5. Leaf birth and death rates of *Puccinellia phryganodes* plants grown in pots in a growth chamber in 1991 and immersed in water of varying salinity. Treatments with the same letter were not significantly different at the 5% level (Steel-Dwass rank tests). Error bars represent $\pm$ 1 SE. Data is represented by shaded areas only.


axillary shoot leaves
main shoot leaves
leaf births / plant / day
leaf deaths / plant / day
0.6
0.5
0.4
0.3
0.2
0.1
0
a
a
b
c
c
c
c
d
c,d
b,c
a,b
a
a
a
0
20
30
40
50
60
70
Salinity of culture solution (g dissolved salts/l)

As salinity increases from 0 to 70 g. dissolved salts/l, the difference between total leaf births and deaths ((TLB - TLD) * study period in days) decreases significantly; this net change in live leaves is not significantly different between 0 and 30 g dissolved salts/l (results of Tukey's tests after ANOVA, $p<0.05$, shown in Fig 6.6). Between 0 and 30 g dissolved salts/l, TLB exceeds TLD and live leaves accumulate, while at salinities greater than 30 g dissolved salts/l, TLD exceeds TLB and live leaves are depleted.

It could be argued that plants of intermediate salinity (30 and 40 g. dissolved salts/l) will tend to have small absolute differences between TLB and TLD because both TLB and TLD are low, but the relative difference (TLB/TLD) may be quite large. This might affect the above conclusions. However, the proportion of leaf births to deaths (TLB/TLD) is significantly higher in plants grown between 0 and 30 g dissolved salts/l, compared to plants grown at 40 to 70 g. dissolved salts/l, similar to the absolute difference between leaf births and deaths; other comparisons are not significant (Steel-Dwass rank tests after Kruskal-Wallis test, $p<0.05$; Fig 6.6). Plants grown between 0 and 30 g dissolved salts/l have TLB/TLD values greater than one and so accumulate leaves, while TLB/TLD values decrease abruptly to near 0 for more saline treatments, indicating a strong relative depletion of leaves (note that the absolute but not relative depletion of leaves increases significantly between 40 and 70 g dissolved salts/l).

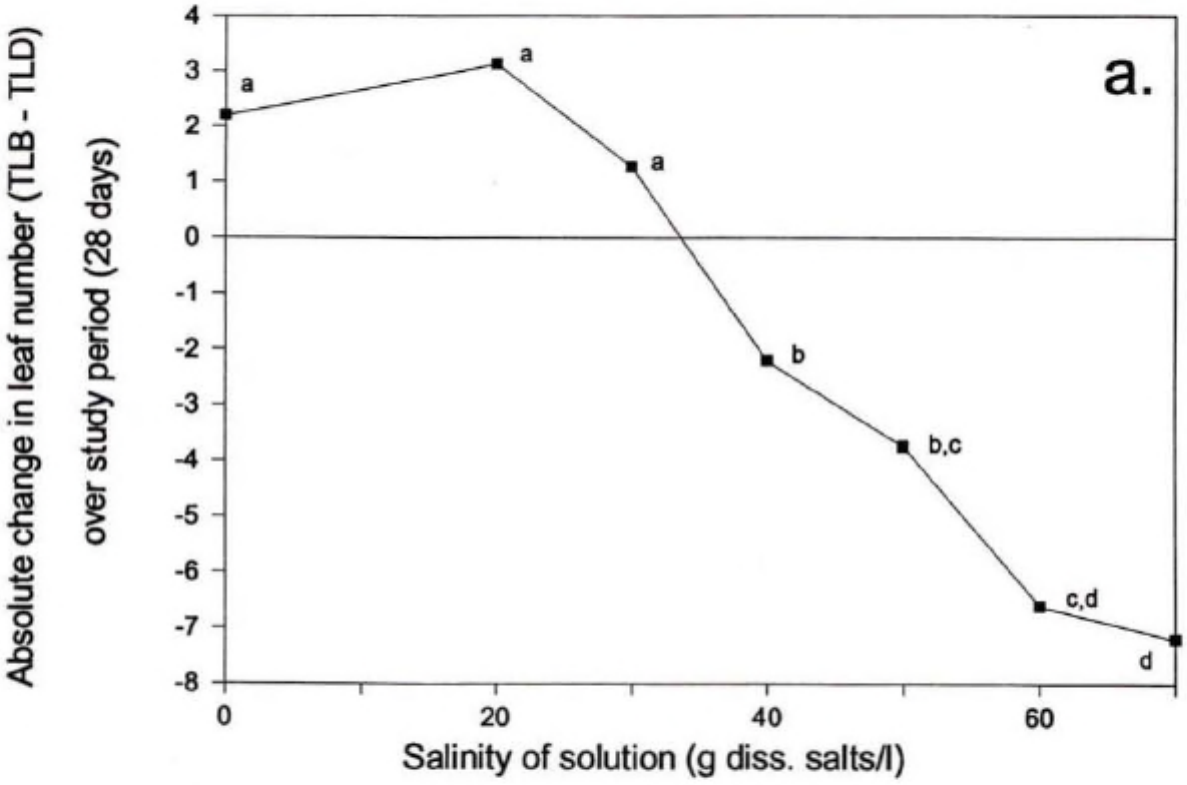
High absolute rates of depletion account for the 40% and 67% plant mortality in 60 and 70 g dissolved salts/l treatments, compared with 0 to 7% in less saline treatments.

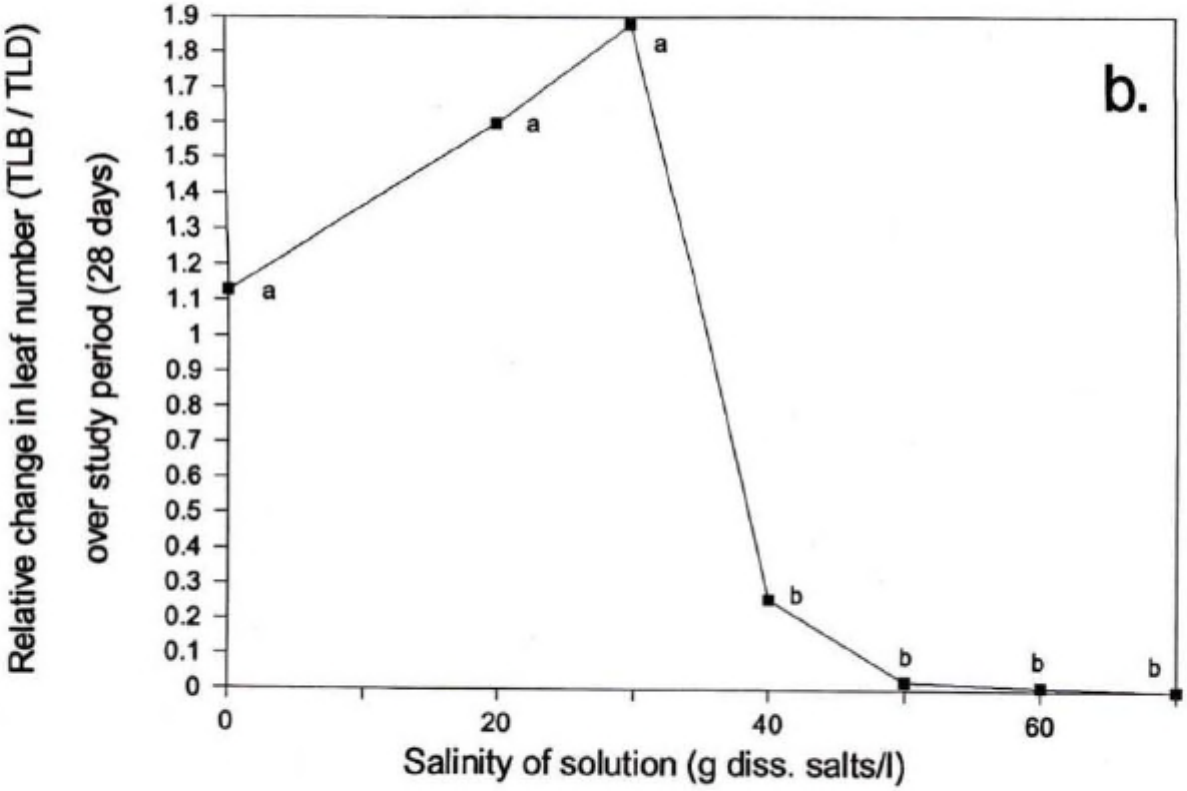
6.4. DISCUSSION

6.4.1 Differential salinity tolerance of *Puccinellia phryganodes* and *Carex subspathacea*

Carex subspathacea appears to be more salt sensitive than *Puccinellia phryganodes*, at least over the range of salinity examined. This is consistent with the observed distribution of

Fig. 6.6. Change in leaf number of *Puccinellia phryganodes* plants calculated either as the difference or quotient of total leaf births (TLB) and total leaf deaths (TLD). Plants were grown in pots in a growth chamber in 1991 and immersed in water of varying salinity. Treatments with the same letter are not significantly different at the 5% significance level (Tukey's tests for TLB-TLD, Steel-Dwass rank tests for TLB/TLD).


a.
Absolute change in leaf number (TLB - TLD)
over study period (28 days)
Salinity of solution (g diss. salts/l)
4
3
2
1
0
-1
-2
-3
-4
-5
-6
-7
-8
0
20
40
60
a
a
a
b
b,c
c,d
d


b.
Relative change in leaf number (TLB / TLD)
over study period (28 days)
Salinity of solution (g diss. salts/l)
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
20
40
60
a
a
a
b
b
b
b

these two species at La Pérouse Bay. *Puccinellia* tends to dominate on the dry non-tidal eastern salt marsh, while *Carex* dominates in the southern salt marsh, where soil salinity is reduced by brackish tide and fresh water stream influences (Fig 1.2). Although differences in the field distributions of *Puccinellia phryganodes* and *Carex subspathacea* have previously been attributed to salinity (Jefferies, 1977; Glooschenko, 1980a; Mason, 1981), the relative salt tolerance of these two species has not been formally examined before.

6.4.2 Response of *Puccinellia* leaf demography to increased salinity

Total leaf births, a measure of growth rate, were either reduced or unaffected in *Puccinellia* when salinity was increased. Most halophytes exhibit a similar response to salinity, although a few have stimulated growth at low salinities (reviewed in Jennings, 1976; Flowers et al., 1977; Ungar, 1991).

When *Puccinellia* plants were grown in a growth chamber and suspended in solutions of 0 to 70 g dissolved salts/l, increasing salinity affected leaf birth and death rates differently. At low salinities (0 to 20 g dissolved salts/l) both leaf birth and death rates were high, implying a rapid rate of leaf turnover. At intermediate salinities (30 and 40 g dissolved salts/l), both leaf birth and death rates were low, indicating a low rate of leaf turnover. At high salinities (> 40 g dissolved salts/l), death rates were high but birth rates were very low, indicating negligible turnover of leaves. Leaf turnover rate, although it was not (and could not be) measured directly, is therefore expected to decrease with increasing salinity. Similar demographic studies of *Triglochin maritima* also found increased salinity resulted in a decrease in leaf turnover through reduced leaf birth and death rates (Rudmik, 1983).

Although the accumulation of live leaves decreased fairly linearly as salinity increased in absolute terms (TLB-TLD), the relative accumulation (TLB/TLD) was constant from 0 to 30 g dissolved salts/l then decreased rapidly between 30 and 40 g dissolved salts/l and was consistently very low from 40 to 70 g dissolved salts/l. These results suggest that with an increase in salinity from 0 to 30 g dissolved salts/l, *Puccinellia* attempts to maintain existing

leaves by reducing both TLB and TLD equally. After 30 g dissolved salts/l, a threshold of tolerance appears to be reached, leaf deaths increase and leaves are depleted. It is possible that leaf depletion is only a short-term response to salinity. In *Triglochin maritima*, for example, leaves were initially depleted for 2 months after salinity was increased, but by 10 months after salinization (in a second experiment), plants had similar rates of leaf accumulation (TLB-TLD and TLB/TLD) as the non-saline controls (Jefferies and Rudmik, 1991). High rates of *Puccinellia* mortality at 60 and 70 g dissolved salts/l, however, indicate that leaf depletion, at least at these salinities, was not reversible. In less saline treatments, plants had had 2 to 4 weeks to adjust to the final salinity of the solutions (leaf birth and death rates are an order of magnitude lower in *Triglochin maritima* than in *Puccinellia*).

This growth chamber experiment indicates that leaf death rates can both be positively and negatively correlated with salinity, depending on the range of salinities examined (positively correlated when leaves are being accumulated, and negatively correlated when leaves are being depleted). In the pot demography experiment in 1991, *Carex* TLD is negatively correlated with salinity (and *Puccinellia* TLD tends to be negatively correlated as well, although this is trend is not quite significant), while in the pot demography experiment in 1992, *Puccinellia* TLD is positively correlated with salinity. For all treatments in the pot demography experiment in 1991 (except 40 g dissolved salts/l for *Carex*), leaves accumulated, while for all treatments (except 0 g dissolved salts/l) in the 1992 pot demography, *Puccinellia* leaves were not accumulating. These patterns are not completely comparable to those of the growth chamber demography. Although TLD tends to be negatively correlated with salinity when leaves accumulate and positively correlated with salinity when leaves are being depleted in both the pot and growth chamber experiments, differences in leaf accumulation and depletion are related only to salinity differences in the growth chamber experiment, but also to weather differences between the pot experiments. Adverse weather may therefore compound salinity stress. Although it was not formally tested in this study, weather and salinity can be said to interact: the reduction in TLB in 1992 compared to 1991 is greater at high salinities than at low salinities. Similar interactions between salinity and adverse weather conditions have been reported earlier (reviewed in

Gale, 1975). In contrast with this study, however, very hot, bright and dry conditions were previously found to exacerbate the effects of salinity.

6.4.3 Resource allocation

In all experiments, growth of axillary shoots was sacrificed before main shoot growth when either *Puccinellia* and *Carex* experienced salinity stress. As argued earlier (Chapter 5), axillary shoots may serve non-essential functions such as vegetative reproduction, horizontal expansion, and avoidance of grazing. In the 0 g diss. salts/l treatment of the 1991 pot experiment, up to 33 axillary shoots were produced on one plant, many of which became unattached from the mother plant and began rooting in the pot. This emphasizes the potential role of axillary shoots as vegetative propagules under favourable conditions. In adverse environmental conditions, rooting and survival of individual axillary shoots may be more reduced than survival and growth of the mother plant as represented by the main shoot (Ungar, 1991, 1978). Resource demands for plant maintenance, on the other hand, are increased because of the "costs" of salinity tolerance (Yeo, 1983), including proline synthesis for osmoregulation in *Puccinellia phryganodes* and other graminoids (Stewart and Lee, 1974; Cargill, 1981). According to life history theory, investment in axillary shoots under adverse salinity or weather conditions, particularly in the absence of grazing, should therefore be selected against. Allocation of resources to sexual reproduction appears to be reduced in many species in saline conditions (Jefferies, 1972; Jefferies et al., 1979b; Ungar, 1987; Jefferies and Rudmik, 1991). In *Triglochin maritima*, for example, increased salinity caused the conversion of shoots with many large leaves into shoots with a few small leaves; only the former bear flowers (Rudmik, 1983). Effects of salinity on allocation of resources to vegetative reproduction are more poorly known.

6.5 **Implications for the positive feedback hypothesis**

These experiments indicate that both *Puccinellia* and *Carex* respond to increased salinity by decreasing total leaf births, preferentially on axillary shoots. This was also

observed for *Puccinellia* in the field (Chapter 5). Growth of *Puccinellia* was much poorer in 1992 than in 1991 in both pots and in the field, emphasizing the importance of weather conditions. Furthermore, there was a greater reduction in *Puccinellia* growth with a given increase in salinity in 1992 than in 1991 for both the field and pot experiments. This implies that adverse weather conditions can interact with salinity stress.

In the field, TLD was negatively correlated with salinity in both 1991 and 1992, although there was high mortality and depletion of leaves in saline bare areas in 1992. Unlike the pot and growth chamber experiments reported here, mortality occurred quickly in bare areas in 1992. Leaf death rates were probably very high over the period plants were dying in the bare areas, but because leaf deaths are averaged over the entire study period, TLD appeared low in these bare areas.

In summary, these experiments demonstrate that salinity can be a main determinant of *Puccinellia* leaf demography in the field. It is possible, however, that a variety of stresses correlated with soil salinity, such as soil moisture or soil oxidation, may also be important in the field.

CHAPTER 7: DISCUSSION

7.1. A positive feedback model of salt marsh destruction

The overall hypothesis of this study was that positive feedback processes between soil salinity and plant growth accounted for the destruction of salt-marsh vegetation at La Pérouse Bay (Section 1.3). In brief, this model suggested that soil salinity is inversely related to above-ground biomass and that plant growth is inversely related to soil salinity. Results from this study conclude that salinity was inversely related to biomass in both 1991 and 1992, and that plant growth (leaf birth rate, plant survivorship) was inversely related to salinity in 1992. Although low biomass sites did not differ from high biomass sites in plant growth in 1991, this was largely because increased axillary shoot growth in the less crowded low biomass sites offset the negative impact of salinity on growth in low biomass sites. Plant growth in bare areas was not examined in 1991, but was probably lower than that of high biomass or low biomass areas (as explained in Chapter 5, the effect of salinity on plant growth is greatest at high salinities while the effect of density on plant growth is minimal at low density, so negative salinity effects should outweigh positive density effects in very saline bare areas). This difference in plant growth between years may reflect differences in weather between years. The summer of 1991 was exceptionally warm and wet, while the summer of 1992 was exceptionally cold and dry (Fig. 1.4). The positive feedback between soil salinity and plant biomass may therefore be greatest in cold, dry years and less important in warm, wet years. Over the last decade there have been a number of exceptionally cold years at Churchill, namely 1982 and 1986 (Scott, 1992). In 1986, a late spring resulted in the staging of large flocks of northward-bound snow geese on the salt marshes of La Pérouse Bay and, consequently, widespread destruction of vegetation by grubbing (D. Hik, pers. comm.). It is possible that this decrease in sward cover, combined with the cold temperatures, may have resulted in a strong positive feedback between soil salinity and plant growth this year.

This positive feedback cycle between soil salinity and plant biomass is predicted to

increase in intensity over time. Several analyses indicate that soil salinity increases exponentially as biomass decreases (Fig. 4.7, 5.3, 5.5). Plant growth (total leaf births) decreases quadratically or exponentially as salinity increases (results from 1991 and 1992; Table 5.3, Fig. 5.9). When biomass is high, a given decrease in biomass will therefore have little effect on either soil salinity or plant growth. As biomass decreases, though, the same decrease in biomass will cause a proportionally greater increase in soil salinity and an even greater proportional decrease in plant growth. This will cause the loss of biomass to accelerate. Such accelerating rates of change are characteristic of systems dominated by positive feedbacks (DeAngelis et al., 1986). There is also a spatial component to the acceleration of the feedback. Soil salinity increases with the size of a bare patch (Chapter 4). As more area becomes unvegetated, the salinity of the unvegetated area will therefore increase, causing the probability of revegetation to decrease. Similarly, in a New England salt-marsh, the area of a bare patch is positively correlated with soil salinity and negatively correlated with plant growth (Bertness, 1991).

Other evidence supports these relationships between soil salinity and biomass. Evaporation rates are lower in vegetated areas than in unvegetated areas (Fig. 4.8), indicating that vegetation modifies soil salinity by reducing evaporation (specifically by either decreasing surface wind speeds or surface temperatures) or otherwise increasing resistance to water movement. Experimentally increasing biomass (by exclosure) led to decreases in soil salinity (Fig. 5.4; Bazely, 1984) indicating that biomass is a cause, not just a consequence, of low soil salinity. Exclosure of salt-marsh vegetation from wildfowl has led to decreased soil salinity in other salt marshes (Joenje, 1985). In controlled experiments, increasing salinity reduced *Puccinellia phryganodes* growth at low salinities by reducing leaf births on axillary shoots but at high salinities by also reducing leaf births on main shoots (Fig. 6.1, 6.4, 6.5). This trend is consistent with the observed response of *Puccinellia* to soil salinity in the field (Chapter 5). It should be cautioned that although plant growth in the field was more strongly related to soil salinity than any of soil water content, soil redox potential or soil bulk density, plant growth may also be strongly related to other soil variables not measured, such as the availability of nitrogen.

Secondary processes may contribute to the feedback. Tough algal crusts are associated with bare and poorly vegetated soils (Fig. 3.2). The presence of such algal crusts has been experimentally shown to reduce graminoid growth (Fig. 5.10). An eroding organic layer also characterizes many unvegetated soils (Fig. 3.2). Although the effects of erosion on graminoid growth were not directly investigated, the frequent association of eroded areas with dead graminoids with exposed roots is noteworthy (Fig. 3.2). The rate of erosion increases exponentially with the proportion of area unvegetated (Marshall, 1973), so this process will accelerate vegetation loss. Bare grubbed areas, compared to vegetated areas, have lower rates of net nitrogen mineralization and a higher ratio of nitrate to ammonium (Wilson, 1993). Since nitrate is more easily leached than ammonium, it has been suggested that more nitrogen will be lost from bare areas than vegetated areas (Wilson, 1983). The availability (ie., supply rate) of nitrogen is therefore expected to be lower in the soils of bare grubbed areas. Of course, competition for nitrogen will be reduced in poorly vegetated areas. On the other hand, nitrogen requirements may be particularly high for plants in saline bare areas, since proline is used as an osmoregulating substance by *Puccinellia* (Cargill, 1981).

Although experimental evidence for the positive feedback relies almost entirely on results for *Puccinellia*, the positive feedback is anticipated to be even stronger for *Carex subspathecea*, since it is the more salt-sensitive of the two species (Chapter 6).

7.2. Implications of the positive feedback model for the future vegetation and goose population at La Pérouse Bay

Over the short term, the positive feedback model predicts that the amount of graminoid vegetation on the salt marsh will continue to decrease, with the rate of vegetation loss possibly increasing over time. As before (Williams et al, 1993), biomass decline may be concentrated in the second half of the brood-rearing period, since the effect of biomass on salinity was greatest in this period (Chapter 4). Since graminoid vegetation is preferred forage for snow geese, and goslings show poor growth on other forage types (Gadallah, 1993), this decrease in graminoid vegetation represents a decrease in availability of quality

forage for the goose population at La Pérouse Bay. Decreases in gosling survival and size over the last decade have been attributed to decreased forage availability at La Pérouse Bay (Cooch et al., 1991; Francis et al., 1992a; Williams et al., 1993). Furthermore, many broods are now dispersing to distant feeding grounds after hatch and gosling growth is higher in such broods (Cooch et al., 1992). Some breeding pairs, however, show strong site fidelity and in recent years have not left the La Pérouse Bay salt marshes, despite low brood survival (Williams et al., 1993). Over the short-term, therefore, further loss of vegetation is expected to increase the probability of dispersal for at least some broods. Over a longer time period, low survival rates in cohorts of goslings (the result of present and future forage loss) will result in a smaller breeding population as the present breeding adults reach the end of their lifespan (at ca. 12-14 years). In short, mid-summer grazing pressure should decrease with further loss of forage.

Reduced goose grazing may not, however, result in revegetation. Presently, grazing has only minor effects on *Puccinellia* growth, even in high biomass areas (Chapter 5). Reduced grazing may reduce soil salinity in high biomass areas but, since goose grazing is presently restricted to high biomass areas (Fig. 5.4, 5.8), similar reduction of soil salinity in low biomass or bare areas is not anticipated. Indeed, experimental exclosure results in a decrease in salinity in high biomass sites but not low biomass or bare areas (Fig. 5.4). Reduction in grazing, therefore, will not slow the conversion of low biomass areas to bare areas. As the area surrounding the islands of high biomass swards become increasingly denuded of vegetation, surface windspeed and hence evaporation rate and soil salinity may increase in the high biomass swards despite no initial reduction of biomass. In this study, for example, soil salinity was shown to increase with the area of unvegetated soil (Chapter 4). Erosion in bare areas may also encroach upon high biomass vegetation. These processes are anticipated to offset any amelioration of soil salinity in high biomass areas by reduced grazing pressure. In any case, both the site-fidelity of certain breeding pairs and the length of time required for the replacement of the present cohorts of breeding adults by depleted gosling cohorts will probably result in the rate of vegetation loss exceeding the rate of grazing pressure reduction. The predicted accelerating nature of the devegetation rate will

exaggerate this asynchrony.

It is unlikely that once *Puccinellia-Carex* vegetation is lost in an area, more halophytic or erosion-resistant species will invade. In areas inland of the salt marsh at La Pérouse Bay, similar loss of *Puccinellia-Carex* vegetation caused by high soil salinity led to invasion by *Salicornia borealis* (Iacobelli and Jefferies, 1991). This area, however, is characterized by a relatively thick organic layer. In the salt marsh itself, *Salicornia* is restricted to the upper end of the marsh (which has the thickest organic layer), and shows no association with the bare degraded areas of the marsh (Fig. 3.2).

The cause of the increase in the goose population, and hence the present loss of vegetation, is ultimately due to human activities (Chapter 1). This loss of vegetation can therefore be termed "desertification" as defined by Dregne (1983): "the impoverishment of terrestrial ecosystems under the impact of [hu]man[s]". As Graetz (1991) notes, the endpoint of a desert is not implied by the term desertification. Similar positive feedback processes have been proposed for desertification in other systems. The Sinai (Egyptian) side but not the Negev (Israeli) side of the Gaza Strip shows obvious loss of vegetation. Otterman (1974) proposed that overgrazing by livestock on the Sinai side has led to the exposure of high-albedo soils and hence lower surface temperatures, which in turn reduced cloud formation over the Sinai region. The reduced rainfall accelerated the desertification process. The same positive feedback is proposed to be the cause of drought and consequent desertification in Sahelian Africa (Sinclair and Fryxell, 1985). An analogous positive feedback involving mid-troposphere cooling by blowing dust has been proposed for the maintenance of Rajasthan desert in India (Bryson and Baerris, 1967). In the Sahel region of Africa, changes in agricultural practices over the last 50 years are argued to have caused widespread overgrazing by livestock (Sinclair and Fryxell, 1985). This vegetation loss through overgrazing is proposed by Graetz (1991) to: a) enhances the formation of soil crusts, leading to reduced water infiltration and loss of soil and nutrient through increased run-off, b) increase loss of soil through wind erosion, and c) increased soil temperatures and evaporation rates. All these factors, Graetz argues, reduce further plant growth, completing

the positive feedback loop. Erosion, in general, can be viewed as a positive feedback cycle, since the increased run-off and reduced organic matter and nutrients associated with erosion will further restrict plant growth (DeAngelis et al., 1986).

At La Pérouse Bay, over a long time period (>50 yr), isostatic uplift and frost heaving of bare areas may cause improved drainage of soils and humus development, which could reduce soil salinity (Hik et al., 1992) and allow revegetation of degraded areas (and colonization of the presently unvegetated newly emerged land). Alternatively, a series of warm wet summers could reduce the positive feedback cycle, and allow some revegetation. If revegetation begins, soil salinities will be further depressed, allowing an accelerating rate of revegetation. In essence, the positive feedback cycle between soil salinity and biomass is reversed. Such a feedback cycle allowing progressive accumulation of a species' biomass is inverse density-dependence when intraspecific, and termed facilitation when accompanied by a change in species composition (Connell and Slayter, 1977). A similar positive feedback cycle of facilitation has been described for secondary succession in a New England salt marsh (Bertness, 1988). As in this study, soil salinities were decreased by increasing plant density, and plant growth (*Juncus gerardi*) was greater in the more vegetated and hence less saline areas. Unlike this study, this facilitation occurred between species (invasion by *Spartina patens* and *Distichlis spicata* facilitated *J. gerardi* growth). DeAngelis et al. (1986) suggest that positive feedbacks, such as facilitation, dominate the early stages of succession, but are increasingly offset by negative feedbacks as succession progresses.

7.3. **Positive feedbacks between soil, plants, and geese at La Pérouse Bay**

At La Pérouse Bay, between 1979 and 1983, grazing by geese was reported to increase net above-ground primary production, NAPP, by 36-106% depending on the year (Cargill and Jefferies, 1984a; Bazely and Jefferies, 1989). Furthermore, shoots from grazed plots had a higher nitrogen content than those from ungrazed plots (Cargill and Jefferies, 1984a; Hik and Jefferies, 1990; Hik et al., 1991). This stimulation of NAPP by grazing occurred because of increased availability of nitrogen for the nitrogen-limited graminoid

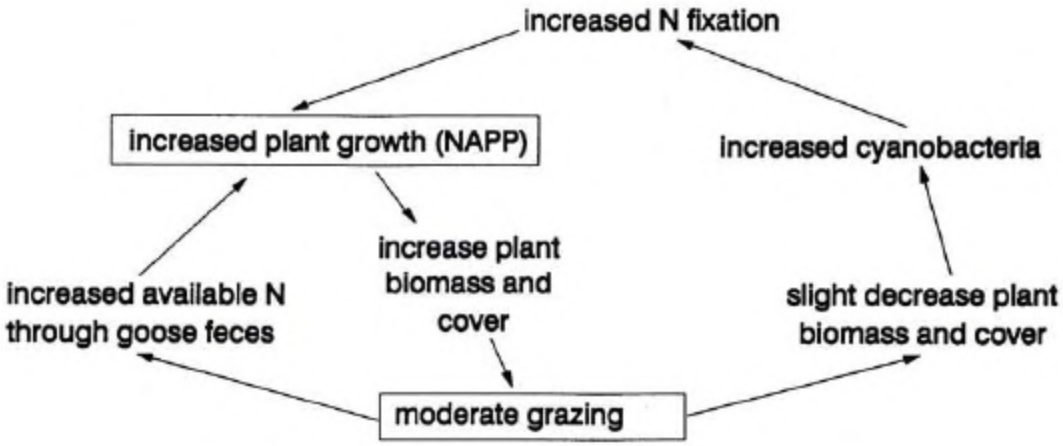
vegetation (Cargill and Jefferies, 1984b). Specifically, grazing increased nitrogen availability because a) conversion of organic nitrogen in plants into soluble nitrogen in goose faeces accelerated the turnover rate of nitrogen in the system (Bazely and Jefferies, 1985; Ruess et al., 1989) and b) lack of plant litter in grazed swards allowed the colonization of sediment by nitrogen-fixing cyanobacteria (Bazely and Jefferies, 1989). There is therefore a positive feedback cycle between NAPP and goose grazing: grazing increases NAPP, and so creates more and better quality forage for further goose grazing (Fig. 7.1).

This stimulation of NAPP was reflected in higher total leaf births in *Puccinellia phryganodes* in 1983 (Bazely and Jefferies, 1989) and *Carex subspathecea* in 1984 (Kotanen and Jefferies, 1987). In the high biomass areas in 1991 and 1992, however, total leaf births of *Puccinellia* were not increased by grazing. This suggests that the positive feedback between NAPP and goose grazing is no longer dominating vegetation dynamics.

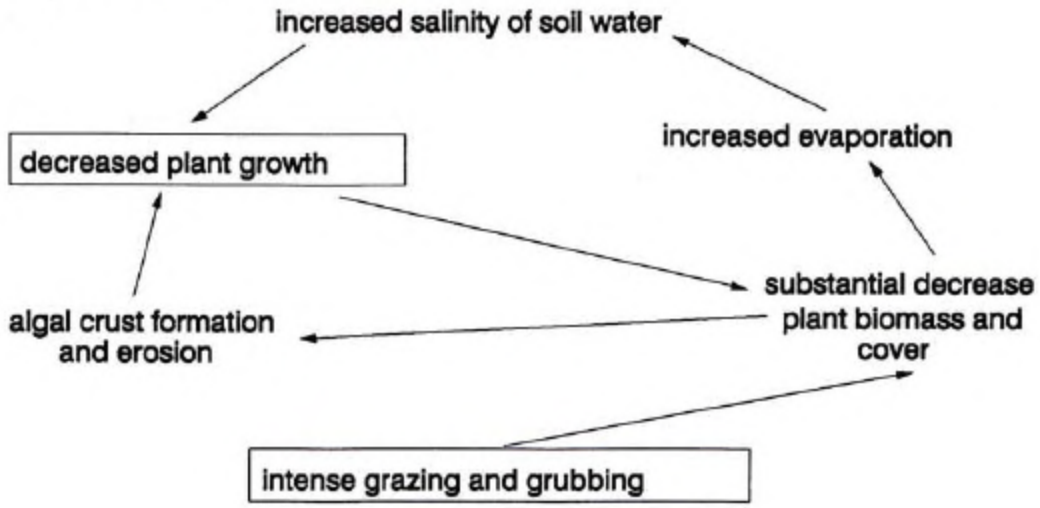
In the positive feedback model between soil salinity and biomass (Fig. 7.1), by contrast, plant growth and hence NAPP is predicted to decrease as a consequence of goose herbivory (overgrazing and grubbing). It should be noted that in this salinity-biomass feedback model, grazing acts as a trigger, not a component, of the model. Although decreased vegetation biomass and cover is predicted to reduce the number of grazing geese utilizing the marsh, this reduction in grazing pressure may not ameliorate soil conditions for reasons described earlier. Also, the salinity-biomass feedback model describes vegetation dynamics of the entire marsh, unlike the NAPP-grazing feedback model which describes only the high biomass areas where goose grazing is concentrated. The two models are integrated in Fig. 7.1.c. In the NAPP-grazing model, a negative feedback between grazing and biomass is illustrated. Grazing is reported to reduce above-ground biomass (ie., standing crop) by about 60-90% (Cargill and Jefferies, 1984a; Bazely and Jefferies, 1989). Goose grazing ceases when plant biomass becomes very low (F. Gadallah, pers. comm.). This negative feedback prevents an indefinite increase in grazing pressure predicted by the NAPP-grazing model alone. A second negative feedback was described by Hik and Jefferies (1990). When grazing pressure increased beyond an optimal value, graminoid meristems were damaged by

Fig. 7.1. The NAPP-grazing (a) and salinity-biomass (b) positive feedbacks are described, compared, and integrated (c). In (c), positive feedbacks occur where the same sign (+ or -) occurs above arrows connecting two variables in both directions, while negative feedbacks occur where different signs occurs above arrows connecting two variables in both directions (DeAngelis et al., 1986). Note that increased grazing leads to increased plant growth (NAPP) in the NAPP-grazing feedback, but leads to decreased plant growth in the salinity-biomass feedback. Also note that grazing is an integral part of the NAPP-grazing feedback but acts only as a trigger in the salinity-biomass feedback. As shown in (c), a negative feedback between grazing pressure and biomass regulates the NAPP-grazing positive feedback (as grazing pressure increases, biomass decreases, causing a decrease in grazing pressure as the herbivore moves to another nearby patch, as predicted by optimal foraging theory). A similar negative feedback may not operate on the same time scale as the salinity-biomass positive feedback. Specifically, increased goose grazing will immediately reduce plant biomass and cover over the entire marsh, but geese may continue to graze areas with less biomass and cover because of fidelity to this salt marsh among other reasons (herbivore movement is now between salt marshes, not just patches within a marsh).

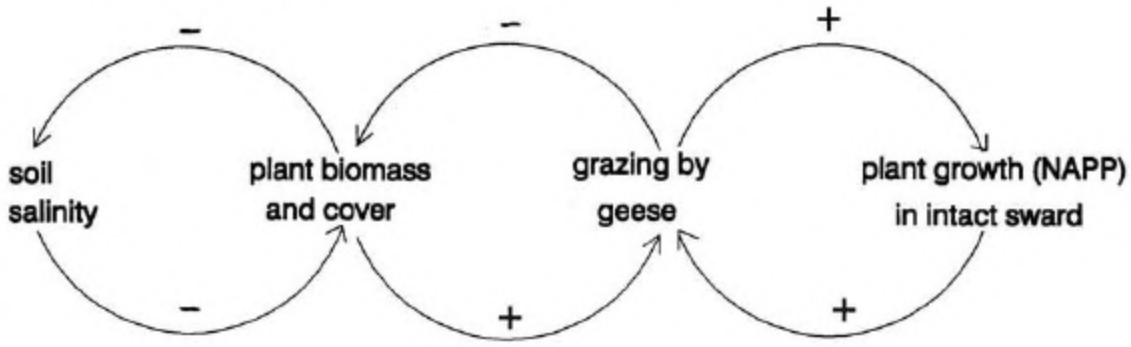
a. NAPP-grazing positive feedback



b. Salinity-biomass positive feedback



c. Positive and negative feedbacks of the salt-marsh

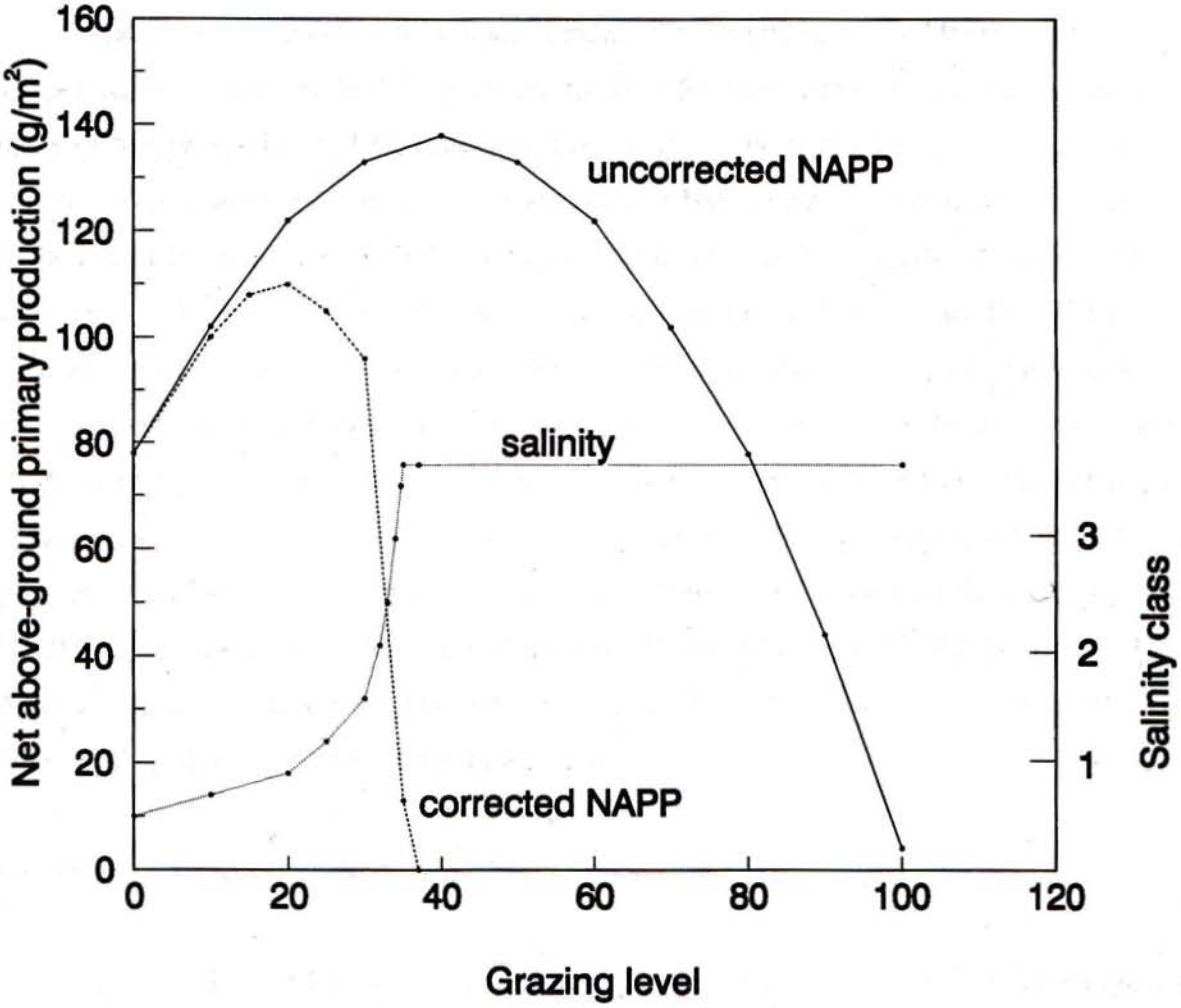


grazing and trampling, and NAPP decreased.

The combined effects of the salinity-biomass positive feedback, the NAPP-grazing positive feedback, and the associated negative feedbacks were examined by a computer model (details described in Appendix 3). This model incorporates data on NAPP response to grazing (Hik and Jefferies, 1990), effects of grazing on *Puccinellia* demography in 1983 (Bazely and Jefferies, 1989) and 1991 (this study), effects of salinity and density on *Puccinellia* demography in 1991 (this study), and the effect of biomass on soil salinity (this study). It is assumed that density *per se* did not affect plant growth between bare and low biomass sites in 1991. General results from this model are expected to be robust because of the heavy reliance on experimental data.

The effect of grazing level on NAPP in a high biomass sward before and after the salinity-biomass feedback is taken into account is illustrated in Fig. 7.2. The units of grazing level correspond to minutes grazed by goslings, as described in Hik and Jefferies (1990), and a grazing level of 10 is assumed to represent 1983 conditions (for reasons described in Appendix 3). Notably, although enhancement of NAPP at intermediate grazing levels occurs both with and without the salinity-biomass feedback, maximum NAPP is less and occurs at a lower grazing level when the salinity-biomass feedback is included. This conclusion is robust for a range of foraging strategies. Furthermore, NAPP decreases abruptly after a certain critical grazing level is reached when the salinity-biomass feedback is included, but decreases slowly without this feedback. The abrupt decrease in NAPP is due to a rapid increase in soil salinity associated with biomass loss. These dynamics occur because the NAPP-grazing feedback predominates at low levels of grazing, while the salinity-biomass feedback predominates at higher levels of grazing. Specifically, the NAPP-grazing feedback results in NAPP increasing with grazing pressure at a decreasing rate (ie., the second derivative is negative, causing a maximum), and so becomes progressively less effective as the grazing level increases (data from Hik and Jefferies, 1990). The salinity-biomass feedback, however, results in salinity increasing with grazing level at an increasing rate (ie., the second derivative is positive), and so becomes progressively more effective as the grazing level

Fig. 7.2. Computer simulation of the effect of grazing level on NAPP both with (corrected NAPP) and without (uncorrected NAPP) the salinity-biomass positive feedback taken into account. Grazing level refers to minutes grazed by captive geese in an experiment by Hik and Jefferies (1990), and a grazing level of 10 is assumed to represent 1983 conditions (rationale discussed in Appendix 3). Salinity classes refer to salinity conditions characterizing high biomass swards (1), low biomass swards (2) and bare areas (3). The model relies heavily on empirical data reported in this and other studies and is described in detail in Appendix 3. Note that the effect of salinity increases with grazing level, and is responsible for the decrease in NAPP at earlier grazing levels than otherwise predicted.


Net above-ground primary production (g/m²)
160
140
120
100
80
60
40
20
0
uncorrected NAPP
salinity
corrected NAPP
0
20
40
60
80
100
120
Grazing level
3
2
1
Salinity class

increases. This is dependent on the negative logarithmic relationships between above-ground biomass and soil salinity and between soil salinity and plant growth reported in this study (Section 7.1). Oesterheld and McNaughton (1991) have argued that the magnitude of NAPP enhancement by grazing should increase with stress. The results from the computer simulation suggest the reverse is true for *Puccinellia phryganodes* experiencing salt-stress.

The herbivore-optimization model predicts enhancement of NAPP (ie., over-compensatory growth) by herbivory at intermediate levels of herbivory but not at low or high levels of herbivory (Dyer, 1975; McNaughton, 1979; Dyer et al., 1982). Although the response of the salt-marsh vegetation at La Pérouse Bay to grazing was consistent with this prediction of the herbivore-optimization model from 1979 to 1986 (Jefferies, 1988a; Hik and Jefferies, 1990), results from 1991 indicate that this is no longer the case. The salinity-biomass feedback may overwhelm the NAPP-grazing feedback at present levels of grazing and grubbing, as suggested by the computer simulation. At least at La Pérouse Bay, over-compensatory growth may occur only for a tightly restricted range of herbivore densities and vegetation states. Other studies have suggested that over-compensatory growth is restricted to systems with certain grazing regimes, leaf demographics, and plant morphologies (Grant et al., 1988; Parsons et al., 1988; Oesterheld and McNaughton, 1991; Jefferies et al., 1993). Over-compensation, therefore, may not be the norm for most ecosystems (Belsky, 1986, 1987; Belsky et al., 1993; Jefferies et al, 1993).

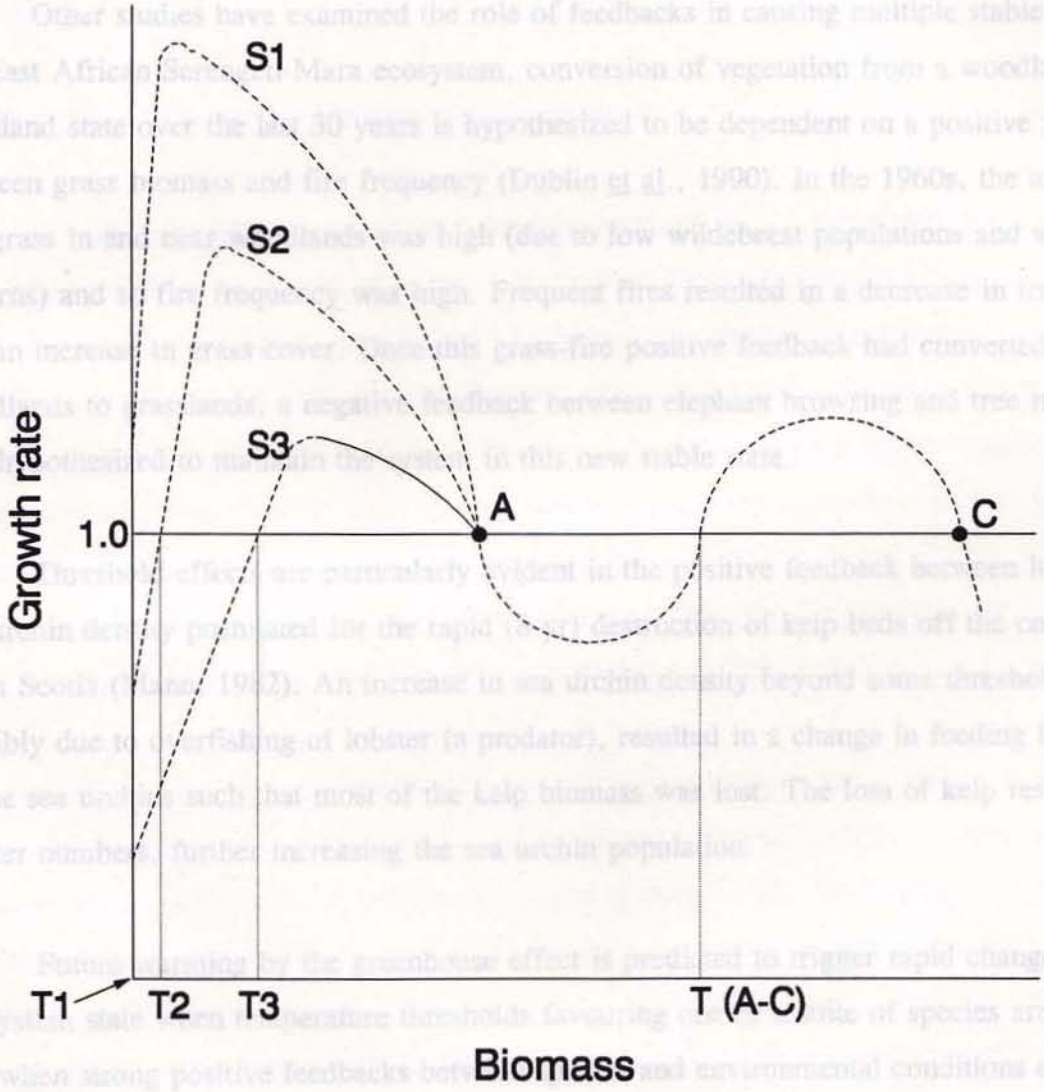
7.4. **Positive feedbacks, threshold effects and stability**

Systems dominated by positive feedbacks often show threshold effects (DeAngelis et al, 1986). Rapid changes in system state occur when these thresholds are crossed. In the vegetation at La Pérouse Bay, a threshold biomass between the *Puccinellia-Carex* state and the *Festuca-Calamagrostis* state has been proposed (Hik et al., 1992). Increases in biomass (by exclosing areas from grazing) beyond this threshold value have been shown to result in the non-reversible attainment of a *Festuca-Calamagrostis* community, while decreases in biomass (by allowing grazing) below this threshold value have been shown to result in a

stable *Puccinellia-Carex* community. This threshold effect is dependent on the *Puccinellia-Carex* NAPP-grazing and salinity-biomass feedbacks previously described, as well as positive feedbacks between organic layer thickness and *Festuca-Calamagrostis* vegetation, and between grazer preference and dicot abundance. The *Puccinellia-Carex* and *Festuca-Calamagrostis* communities are alternative stable states in this model.

Results from this study indicate that bare degraded areas constitute a third non-aquatic salt marsh state in addition to the *Puccinellia-Carex* and *Festuca-Calamagrostis* states. Bare degraded areas are not considered a stable state by Hik et al. (1992) because revegetation in partially vegetated, grubbed plots was rapid in 1986 and 1987. Recent decreases in biomass, however, are not consistent with a transition to either the *Puccinellia-Carex* or *Festuca-Calamagrostis* states (Fig. 2 in Hik et al., 1992). The results of this study indicate that growth is now severely restricted in bare areas. It is proposed that bare degraded areas now constitute a third stable state in the salt marsh. This implies that a threshold in biomass exists between the bare degraded state and the *Puccinellia-Carex* state. As the strength of the salinity-biomass feedback increases, the growth rate of low biomass *Puccinellia-Carex* vegetation is expected to decrease and so cause this threshold to occur at higher values of biomass (Fig. 7.3). As the biomass threshold value increases, the probability of a given loss of biomass crossing the threshold also increases, so the persistence of the *Puccinellia-Carex* state is reduced. The revegetation rate (the slope of growth rate over biomass in Fig 7.3) also decreases as the biomass threshold increases, so the resilience of the *Puccinellia-Carex* state to biomass loss also decreases. In terms of persistence and resilience (as defined by Pimm, 1984) at least, the salinity-biomass feedback therefore reduces the stability of the *Puccinellia-Carex* state. Over the last decade such an increase in the strength of the salinity-biomass feedback and consequent reduction in the stability of the *Puccinellia-Carex* state may have occurred. A test of the above hypothesis would involve the experimental removal of a fixed number of graminoid plants in *Puccinellia-Carex* swards representing a range of biomass. Revegetation would be predicted in areas of higher biomass but not in areas of lower biomass.

Fig. 7.3. Effect of increasing the strength of the salinity-biomass feedback (increases from S1 to S2 to S3) on the dynamics of vegetation at La Pérouse Bay. Growth rate for a given year (x) is defined as the quotient of biomass of the next year (x+1) over biomass of the given year (x). Growth rates greater than 1 therefore indicate that biomass is increasing between successive years, while growth rates less than 1 indicate that biomass is decreasing between successive years. Thresholds (T) occur between stable states of no biomass (biomass=0) and *Puccinellia-Carex* swards (A) and between stable states of *Puccinellia-Carex* swards (A) and *Festuca-Calamagrostis* swards (C). As the salinity feedback increases in strength (from S1 to S3), the thresholds (T1 to T3) between no biomass and A occur at progressively greater values of biomass. The effect of salinity feedback on the threshold between A to C, T(A-C), is not known. Modified from Fig. 4 of Hik et al., 1992.


S1
S2
S3
A
C
1.0
Growth rate
T1
T2
T3
T (A-C)
Biomass

Hik et al. (1992) suggest over a time frame of 10-50 years, the *Puccinellia-Carex* state may disappear from the present salt-marsh as a result of isostatic uplift. Similarly, over the long term, isostatic uplift and weather events may allow the bare degraded state to disappear from the present salt-marsh, as argued earlier.

Other studies have examined the role of feedbacks in causing multiple stable states. In the East African Serengeti-Mara ecosystem, conversion of vegetation from a woodland to grassland state over the last 30 years is hypothesized to be dependent on a positive feedback between grass biomass and fire frequency (Dublin et al., 1990). In the 1960s, the amount of dry grass in and near woodlands was high (due to low wildebeest populations and weather patterns) and so fire frequency was high. Frequent fires resulted in a decrease in tree density and an increase in grass cover. Once this grass-fire positive feedback had converted woodlands to grasslands, a negative feedback between elephant browsing and tree mortality was hypothesized to maintain the system in this new stable state.

Threshold effects are particularly evident in the positive feedback between lobster and sea urchin density postulated for the rapid (8 yr) destruction of kelp beds off the coast of Nova Scotia (Mann, 1982). An increase in sea urchin density beyond some threshold value, possibly due to overfishing of lobster (a predator), resulted in a change in feeding behaviour of the sea urchins such that most of the kelp biomass was lost. The loss of kelp restricted lobster numbers, further increasing the sea urchin population.

Future warming by the greenhouse effect is predicted to trigger rapid changes in ecosystem state when temperature thresholds favouring one or a suite of species are crossed and when strong positive feedbacks between species and environmental conditions exist (Pastor and Post, 1988). Specifically, positive feedbacks between carbon utilization in primary production and soil nitrogen availability (Hobbie, 1992) were predicted to cause species change and biomass increases at the current boreal/northern hardwood border (Pastor and Post, 1988). In a past period of climate warming (4000-5000 years ago), for example,

changes from tundra to black spruce forests in Canada occurred remarkably quickly (MacDonald et al., 1993). Pastor (1993) suggests this is the result of positive feedbacks between spruce density and each of seed dispersal (cold temperatures cause a stunted growth form which has a low fecundity, limiting spruce density), litter nutrient content (spruce litter is nutrient-rich and may accelerate nutrient cycles, promoting spruce growth) and fire frequency (spruce litter is more flammable than that of tundra, and fire promotes cone opening).

7.5. **Asynchrony in arctic herbivore-plant ecosystems**

An important determinant of the future dynamics of the La Pérouse Bay graminoid-goose system will be the degree of asynchrony between plants and herbivore on two time scales. Over a short period of time (up to 10 years), goose density is predicted not to decrease as quickly as the plant biomass because of a) the accelerating nature of the positive feedback, b) feeding site-fidelity of some geese, and c) depletion of younger cohorts exceeds that of older breeding cohorts. Such an asynchrony is predicted to result in further loss of vegetation. Creation of new salt-marsh vegetation may take a long period of time (50 years?), so the plant colonization or revegetation rate rather than the intrinsic rate of increase of the goose population may limit further goose densities on this marsh.

The dynamics of some other arctic herbivore-plant systems show similar types of asynchrony. Caribou and reindeer grazing of lichen pastures and associated trampling effects can cause severe destruction of these communities (Pegau, 1970). Such damaged lichen communities may take on the order of 15 to 20 years without grazing for recovery (Palmer and Rouse, 1945; Semyenov-Tyan-Shanskiy, 1977, in Chernov, 1985; Chernov, 1985). Jefferies et al. (1993) suggest, on the basis of recent radio-collar data on caribou movements, that caribou may not return to a given area for at least several years to allow regrowth of forage. On the small island of St. Matthew in the Bering Sea, reindeer were not able to move to ungrazed areas. The subsequent destruction of lichen pastures caused a dramatic crash in the reindeer population 20 years after the introduction of the original animals (Klein, 1968).

Even 22 years after the crash, lichen standing crop was only 10% of that on a nearby ungrazed island (Klein, 1987). Similar destruction of lichen communities is thought to be responsible for the crash in reindeer on St. Paul Island (in the Pribilof group) 40 years after their introduction (Scheffer, 1951). Notably, on the sub-antarctic island of South Georgia, a reindeer population, first introduced in 1911, increased in numbers up to 1957 and then declined but did not crash over the period 1957-1976 (Leader-Williams, 1980). The decline was attributed to over-grazing of the primary forage species, tussock grass. The difference in population dynamics between reindeer populations on South Georgia and those on St. Paul and St. Matthew has been attributed to the resilience and fast growth rates of tussock grass compared to that of lichens (Leader-Williams, 1980).

Oscillatory changes in population numbers of arctic microtines have similarly been hypothesized to reflect asynchronies between slow plant growth and fast animal production rates (Tast and Kella, 1971; Jefferies et al., 1992). This is supported by correlations between high microtine densities and both high-quality forage (Batzli, 1983; Batzli and Henttonen, 1990) and flowering (Laine and Hettonen, 1983; but see Oksanen and Erikson, 1987). Recent evidence suggests that an asynchrony between the slow growth of forage in predator-free spaces and the relatively rapid growth of the snowshoe hare population may be important in arctic snowshoe hare cycles (D.Hik, unpublished data).

In summary, the asynchrony between slow plant growth and the rapid growth of some herbivore populations may be an important feature of certain dynamic arctic herbivore systems (eg., the "low input" systems of Jefferies et al, 1992). In other systems, high plant growth rates following grazing may result in less locally variable herbivore densities (eg., the "high input" systems of Jefferies et al., 1992). The graminoid-goose system at La Pérouse Bay may have converted from the latter type of system to the former.

APPENDIX 1: AN ANOVA TABLE FOR THE LEAF DEMOGRAPH OF PLANTS GROWING IN A SALT MARSH IN 1991 (A SUPPLEMENT TO CHAPTER 5)

The following ANOVA table uses TLB data (square-root transformed) for illustration, but the general layout (ie., main effects and interaction variables, degrees of freedom, denominator mean square) is identical to ANOVA tables for TLD, MSLB, MSLD, ASLB, and ASLD. The MANOVA table (overall effect of all these demographic parameters) is constructed similarly, except that type III sum of squares are used, and the p value is generated by Wilk's Lambda.

In the table below, in addition to the standard statistical abbreviations, the following abbreviations are used: T (treatment), S (site), G (graze), O (origin), R (replicate). Please refer to Chapter 5 for description of the experimental design.

source	df	SS	MS	DMS	F	P
T	3	0.6330	0.2110	S(T)	4.64	0.011
S(T)	24	1.091	0.04550	R(OGST)	2.58	0.0004
G	1	0.03140	0.03146	GS(T)	2.66	0.12
GT	3	0.02182	0.007273	GS(T)	0.61	0.61
GS(T)	24	0.2840	0.01183	R(OGST)	0.67	0.87
O	1	0.01030	0.01030	OS(T)	0.50	0.49
OT	3	0.01573	0.005243	OS(T)	0.25	0.86
OS(T)	24	0.4972	0.02072	R(OGST)	1.18	0.28
OG	1	0.02520	0.02519	OGS(T)	1.80	0.19
OGT	3	0.01229	0.004100	OGS(T)	0.29	0.83
OGS(T)	24	0.3354	0.01400	R(OGST)	0.79	0.74
R(OGST)	112	1.973	0.01762	-----	----	----

APPENDIX 2: INTERVAL-BASED DEMOGRAPHIC PARAMETERS FOR GRAMINOID GROWTH IN A SALT-MARSH in 1991 and 1992 (A SUPPLEMENT TO CHAPTER 5)

METHODS

Demographic methods for plants in high and low biomass sites in 1991

General methods are described in Chapter 5 under this heading. Calculated interval-based demographic parameters included main shoot leaf birth rate (MSBR), main shoot leaf death rate (MSDR), axillary shoot leaf birth rate (ASBR), axillary shoot leaf death rate (ASDR), main shoot leaf lifespan (MSLL) and axillary shoot leaf lifespan (ASLL).Interval-based demographic parameters could not be calculated for all plants. In particular, early plant death, late or non-production of axillary shoots, birth of less than two leaves, and a fast leaf death rate all prevented calculation of certain demographic parameters. Since there were unequal sample sizes, a regression approximation to ANOVA was used (SAS, general linear model procedure, type III SS). For main shoots, data was available for 198 of 224 plants, so a regression approximation to ANOVA could be used. For axillary shoots, however, ASBR and ASLL data was available for only 103 plants, because many plants produced no axillary shoots or axillary shoots with too few leaves for interval-based computations. Only a small percentage (21%) of plants had ASDR data, including only 5 of 56 plants in high biomass sites, so ASDR was not examined. The full model was fitted to MSBR, MSDR, and MSLL data, but since the degrees of freedom needed by the full model exceeded the number of ASBR and ASLL observations, the latter two parameters were fitted to a reduced model (effect of grazing not examined). All data conformed to ANOVA assumptions.

Demographic methods for plants in high biomass, low biomass, and bare sites in 1992

General methods are described under this heading in Chapter 5. Most plants did not produce axillary shoots. Therefore, ASBR, and ASDR were not calculated. Since there is only one value of MSLL possible in a three census study, MSLL was not calculated. Both MSBR and MSDR can, however, have a wide range of values, so these were calculated where possible.

RESULTS

Interval-based parameters are not synonymous with their seasonal counterparts ($r=0.59$ to 0.75). The following results are arranged under identical numbered headings as those used in Chapter 5 and differences with the results of Chapter 5 are discussed. For full details of statistical analyses refer to the appropriate heading in Chapter 5. Some sections of Chapter 5 are not represented because of restrictions on the interval-based demographic data sets discussed above.

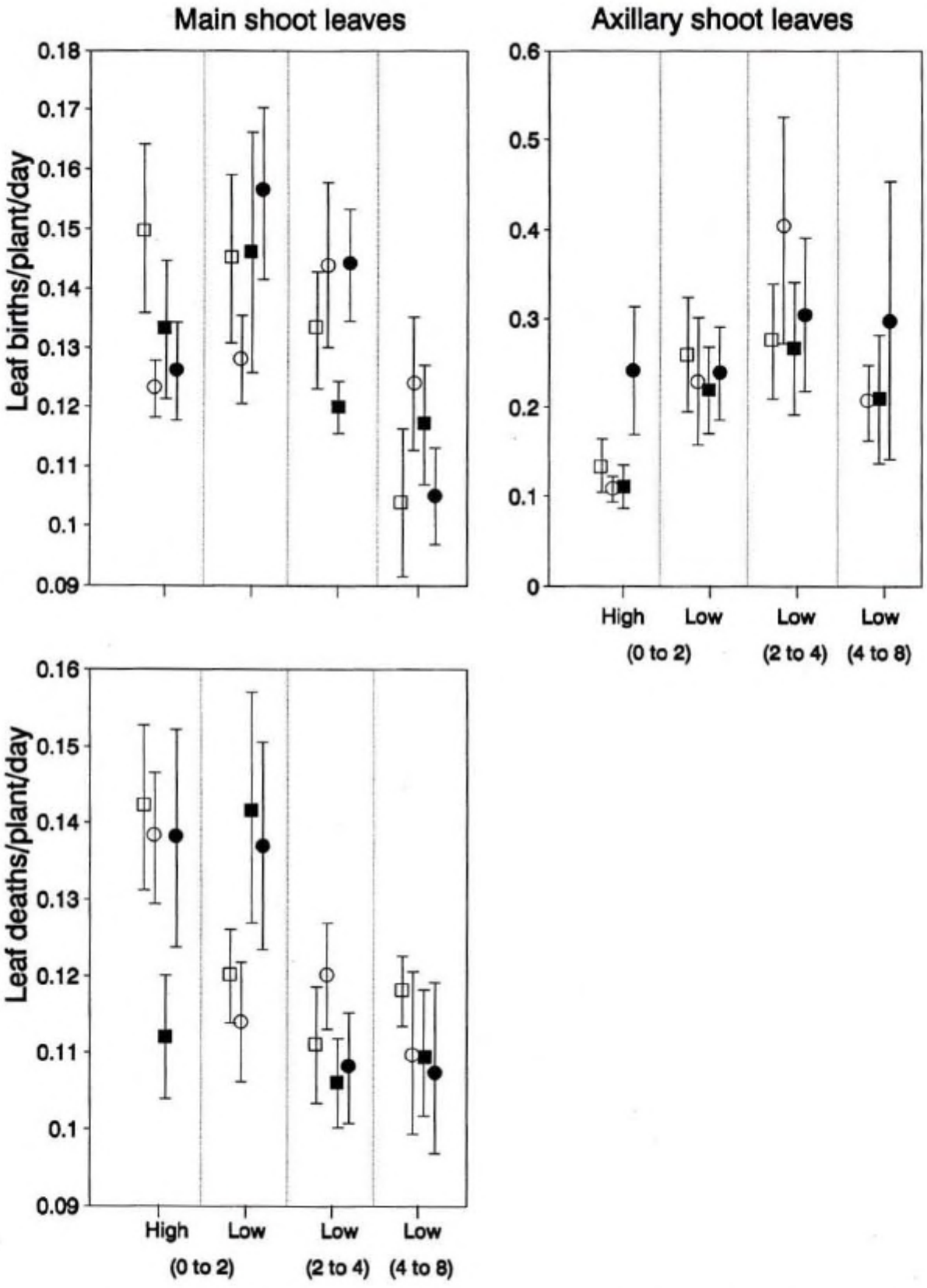
5.5.3. Leaf demography did not differ between plants in high and low biomass sites in 1991, but did differ in 1992 between plants in high and low biomass sites, and between plants in low biomass and bare sites.

5.5.3.1 1991 In 1991, a significant treatment effect existed for MSBR and MSDR (regression approximation of ANOVA, $p<0.05$; Fig. A2.1). This treatment effect was almost significant for MSLL (regression approximation of ANOVA, $p<0.10$; Fig. A2.2). Site effects were not significant for MSBR, MSDR, or MSLL (regression approximation of ANOVA, $p>0.05$). No interactions involving treatment were significant for MSLL (regression approximation of ANOVA, $p>0.05$). Interactions between treatment and grazing and treatment and origin are described below for MSBR and MSDR, respectively. Neither treatment, site, plant origin, or any interactions between them had a significant effect on ASBR or ASLL (regression approximation to ANOVA, $p>0.05$; Fig. A2.1,2).

On average, plants in high biomass sites did not have a significantly different MSBR than those in low biomass sites (F tests, low biomass treatments averaged, $p>0.05$). This result is similar to that obtained with seasonal demographic data. By contrast, MSDR was significantly higher in high biomass sites, and, consequently, MSLL was significantly lower in high biomass sites (F test, low biomass sites averaged, $p<0.01$).

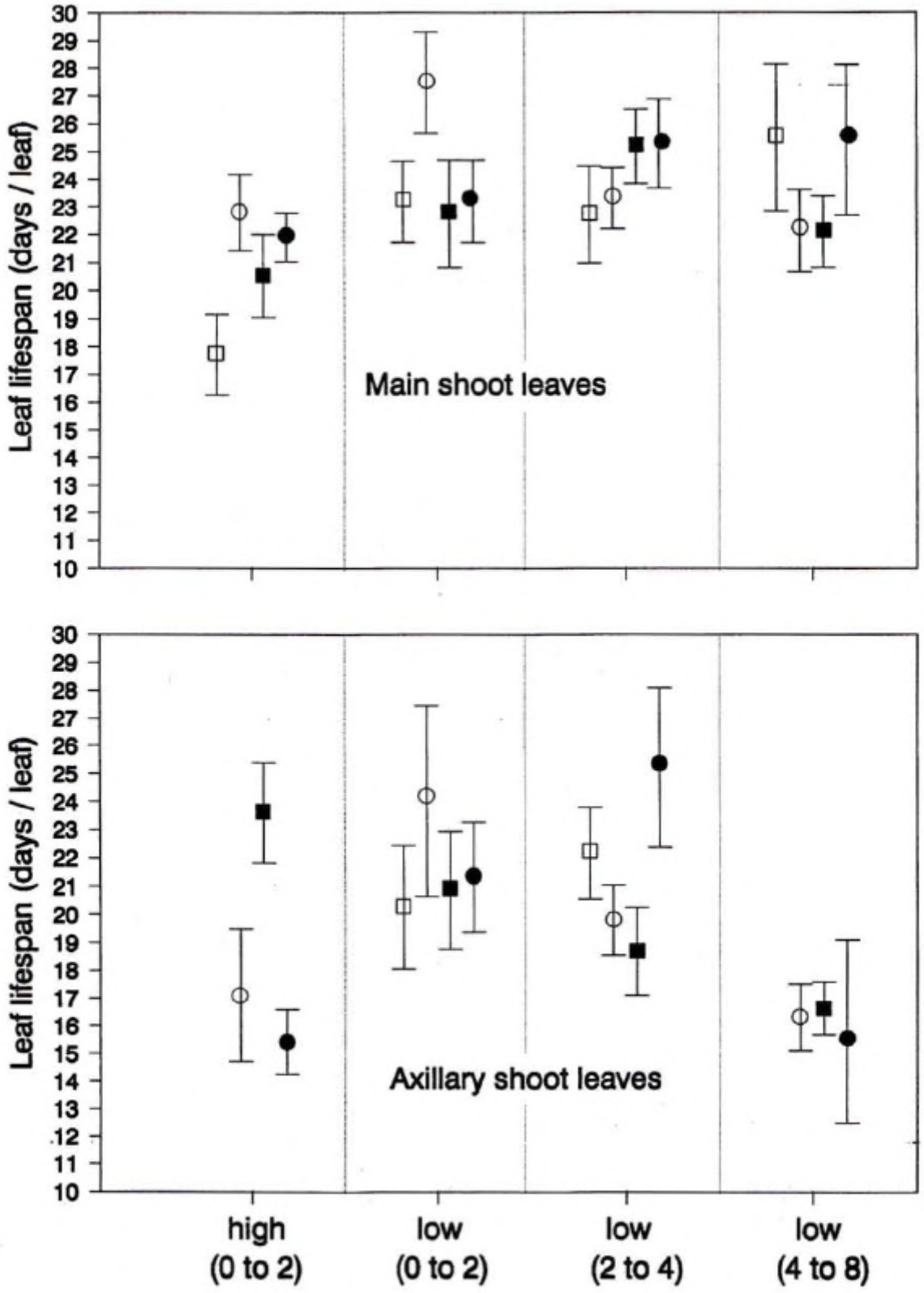
5.5.3.2 1992 Similar analyses cannot be performed for 1992. At least two leaf births need to occur over the study period for calculation of interbirth intervals and hence main shoot birth

Fig. A2.1. Interval-based leaf birth and death rates for *Puccinellia* plants of high biomass origin (squares), low biomass origin (circles), in grazed (open symbols) and exclosed (closed symbols) areas of sites in 1991. Error bars are $\pm$ 1 SE.



Site biomass (high or low) and sodium concentration of soil water (g/l)

Fig. A2.2. Interval-based leaf lifespans for *Puccinellia* plants of high biomass origin (squares), low biomass origin (circles), in grazed (open symbols) and exclosed (closed symbols) areas of sites in 1991. Error bars are $\pm$ 1 SE.



Site biomass (high or low) and sodium concentration of soil-water (g/l)

rate (MSBR): this condition is not met by most plants in the four more representative low biomass sites or in the bare sites.

5.5.4. Grazing and plant origin had complex effects on leaf demography in 1991, and grazing increased leaf deaths in 1992.

5.5.4.1 1991 A significant interaction between treatment and grazing category existed for MSBR (regression approximation of ANOVA, $p<0.05$). Exposure to grazing increased MSBR in high biomass sites, but this effect of grazing does not occur or is reversed in low biomass sites (F tests, $p<0.05$).

A significant interaction between treatment and plant origin existed for MSDR (regression approximation of ANOVA, $p<0.01$). In high biomass sites, high biomass origin plants tended to have higher MSDR than low biomass origin plants, while the reverse was true in low biomass sites (F test, $p<0.05$). Furthermore, this effect of origin in low biomass sites was greatest in sites of low salinity (0 to 2 g/l Na), and negligible in more saline sites (2 to 4 and 4 to 8 g/l Na; F test, $p<0.05$).

Similar results were not reported for the seasonal demographic parameters.

5.5.4.2 1992 See section 6.2 of this appendix.

5.5.5. Within the low biomass sites, leaf demography was a function of both salinity and plant density in 1991.

Among low biomass sites, plants in the most saline sites (4 to 8 g/l Na in extracted soil water) had a significantly lower MSBR than those in the less saline sites (0 to 2 and 2 to 4 g/l Na; F tests, $p<0.05$). Although plants in the moderately saline low biomass sites (2 to 4 g/l Na) had a lower MSBR compared to plants in the least saline low biomass sites (0 to 2 g/l Na), these differences were not significant (F tests, $p>0.05$). In low biomass sites,

MSDR decreased significantly between plants in the least saline (0 to 2 g/l Na) and in moderately saline (2 to 4 and 4 to 8 g/l Na) sites (F test, $p<0.05$), but did not decrease further between plants in moderately (2 to 4 g/l Na) and very saline (4 to 8 g/l Na) sites (F test, $p>0.05$). Similar results were reported for the seasonal demographic data. By contrast, MSLL was constant across salinity categories in low biomass sites (F tests, $p>0.05$).

MSBR and MSDR were significantly and negatively correlated with the sodium concentration of extracted soil water ($r=-0.71$ and -0.43, respectively, $n=21$) and the correlation of ASLL with sodium concentration was almost significant ($r=-0.439$, $n=20$, $p<0.06$). The interval-based variables MSLL and ASBR were not significantly correlated with sodium concentration.

The stepwise regressions (methodology described under this heading in Chapter 5) with interval-based demographic parameters confirm the importance of density on axillary shoot production indicated by similar regressions with seasonal demographic parameters. The only significant explanatory variable for ASBR was density (logarithmic form, $r^2=0.64$), and both sodium concentration and density were significant explanatory variables for ASLL ($r^2=0.39$). Conversely, density was not a significant explanatory variables for MSDR; sodium concentration (logarithmic form) and water content were significant explanatory variables ($r^2=0.35$). Although density (logarithmic form) was, in addition to sodium concentration, a significant explanatory variable for MSBR ($r^2=0.66$), the correlation between MSBR and density ($r=-0.27$, NS, logarithmic form of density) was less than that of density with any of ASLB, ASLD, ASBR or ASLL ($-0.33<r<-0.80$, linear or logarithmic form of density). Lastly, no significant explanatory variables existed for MSLL. In all regression equations, the effect of increasing sodium concentration or density was a decrease in the demographic parameter.

5.5.6. Within sites of similar soil salinity, leaf demography of axillary shoots was a function of plant density.

5.5.6.2 1992 In 1992, only MSBR and main shoot death rate (MSDR) was computed for the four high high biomass sites and two low biomass sites (sites 5 and 6) with similar (low) soil salinity. There is only one possible value of main shoot leaf lifespan (MSLL) with the three census dates of this study.

Overall, the effect of both site and grazing was significant, but not the site by grazing interaction, in the six sites (four high biomass sites and two low biomass sites; MANOVA, Wilks Lambda). For MSBR, however, neither site nor grazing effects (or their interaction) were significant (ANOVA, $p>0.15$) similar to results for the seasonal parameter MSLB (7.2, Chapter 5).

For MSDR, the effect of site was significant ($p<0.05$) and the site by grazing interaction almost significant ($p<0.06$), but the effect of grazing was not significant (ANOVA, $p>0.09$). The high biomass sites had significantly higher MSDR values than the low biomass sites (F test, $p<0.005$); the remainder of the site effect is not significant. The average MSDR ($\pm$ SD) of plants in high biomass sites was 0.159 ($\pm$ 0.038) leaves/plant/day, versus 0.141 ($\pm$ 0.036) leaves/plant/day in two low biomass sites. As in the analyses of seasonal demographic data (7.2, Chapter 5), density affects plant performance. Analyses of seasonal demographic data, however, indicated that density reduced ASLB, though, rather than affecting main shoot leaf deaths. The almost significant interaction between site and grazing is largely due to a reversal of the effect of grazing in the two low biomass sites (F test, $p<0.05$); the remainder of the interaction term does not approach significance.

5.5.7. In regression equations involving sites from all biomass categories, both salinity and density were important determinants of leaf demography in both 1991 and 1992.

5.5.7.1 1991 Stepwise regression equations were calculated for data averaged within sites as

described in Chapter 5 under this heading. The resultant regression equations can be summarized as follows. Biomass or biomass category are the only explanatory variables for ASBR and MSLL. Both sodium concentration and density are significant explanatory variables for ASLL, MSBR, and MSDR (water content is also a significant but minor explanatory variable for the latter). Density was therefore more important in interval-based than seasonal main shoot demography (although, as before, correlations between density and either MSBR or MSDR are lower than correlations between density and axillary shoot parameters). Although the effect of density in these regression equations is non-linear, MSBR generally decrease as density increases, while MSDR increases as density increases (for the range of densities encountered). The consequence of negative effect these trends is a reduction in MSLL between high and low biomass sites.

It could be argued that by averaging data for up to eight plants per site, important information on the effect of grazing and origin is lost. To examine this possibilty, regression models were computed as described under this heading in Chapter 5. Again ASBR and ASLL were not examined because of paucity of these data in high biomass sites. As before, only density and sodium were significant for MSBR. However, a significant and negative origin by density interaction existed for MSDR, indicating that high origin plants had a greater MSDR than low biomass origin plants in high biomass sites, but not in low biomass sites. This is identical to the result found in the earlier ANOVA analysis. Also significant was a grazing by origin by density interaction existed for MSLL: grazed plants of low biomass origin had longer MSLL in high density sites but not low density sites. Together, these two interactions imply that main shoot leaf turnover is faster for high biomass origin plants in high biomass sites, and for low biomass origin plants in low biomass sites. Similar results were not obtained with seasonal demographic data.

5.5.8. *Carex* growth was also greater in high biomass areas than in bare areas

Interval-based demographic parameters (main tiller leaf birth and death rates, analogous to MSBR and MSDR) could only be calculated for *Carex* plants in high biomass

sites; similar to *Puccinellia*, plants in bare sites did not produce enough leaves for calculation of birth rates of lifespan of leaves on attached tillers (analogous to ASBR and ASLL), and leaf death was too fast for calculation of death rates of leaves on attached tillers (analogous to ASDR). Neither main tiller leaf birth or death rates differed between sites (ANOVAs, $p>0.05$). The mean value ($\pm$ SD) of the main tiller leaf birth rate was 0.128 ($\pm$ 0.083, n=35) leaves/plant/day, lower than the MSBR value for *Puccinellia* (same grazed areas) of 0.146 ($\pm$ 0.053, n=70) leaves/plant/day. A similar result was obtained for the seasonal demographic parameter TLB. The mean value of the main tiller leaf death rate was 0.154 ($\pm$ 0.097, n=37) leaves/plant/day, similar to the MSDR value of 0.154 ($\pm$ 0.038, n=66) leaves/plant/day for *Puccinellia*. By contrast, the seasonal demographic parameter TLD was lower in *Carex* than *Puccinellia*, perhaps reflecting the higher mortality rate of *Carex* (interval-based parameters are not calculated for plants which die during the study period).

APPENDIX 3: A MODEL OF GRAZER-DEPENDENT POSITIVE FEEDBACKS IN SALT MARSH VEGETATION

Introduction

The salinity-biomass and NAPP-grazing positive feedbacks act in opposite directions. An increase in grazing pressure causes, in the NAPP-grazing feedback, an increase in plant growth (NAPP), while in the salinity-biomass feedback this triggers a decrease in plant growth (NAPP). Previously, these feedbacks have been studied in isolation. What happens if they are put together? One way to examine this is by modelling.

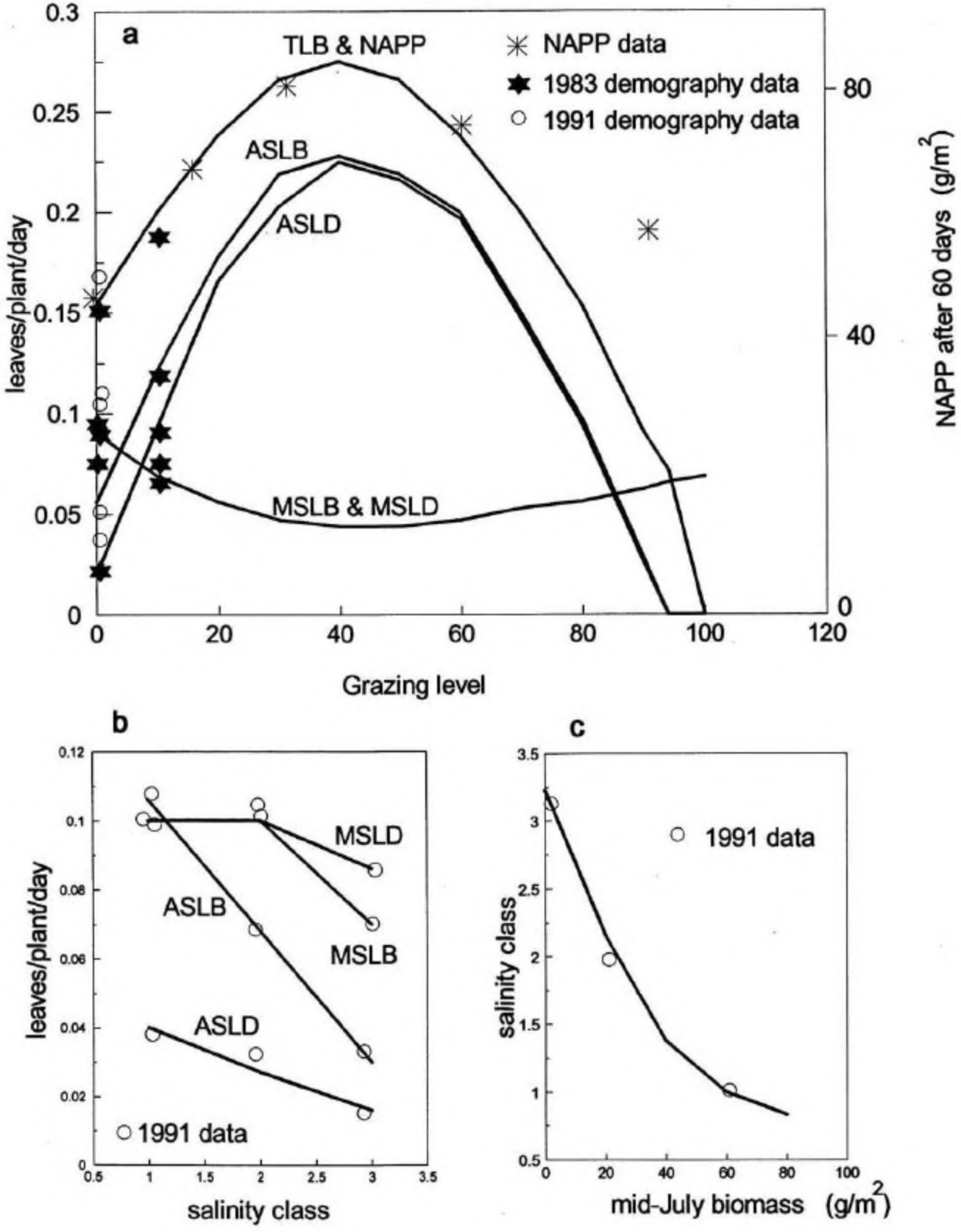
Components of the model

1) Grazing and graminoid growth. Although grazing pressure increases NAPP, this effect diminishes with increased grazing pressure. In a 1985 experiment, captive goslings were allowed to graze an enclosed patch of vegetation for various periods of time and NAPP measured (Hik and Jefferies, 1990). NAPP peaked at intermediate grazing periods, and was low at short and long grazing periods (Fig. A3.1.a). A quadratic curve describes the response of NAPP (after 60 days, approximately 1 growing season) to grazing (in minutes), as follows:

$$47*(\text{NAPP} - 77) = (\text{grazing level} - 40)^2 \qquad \text{[eq. 1]}$$

This can be related to graminoid growth under field conditions. Under field conditions, other researchers have shown that from 1979 to 1983 naturally grazed plots had about 35 to 40 g/m^2 more NAPP than ungrazed (exclosed) plots by the end of August (Cargill and Jefferies, 1984; Bazely, 1984). In 1983, this meant grazed plots had about 1.36x the NAPP of ungrazed plots. In the captive gosling experiment, NAPP was about 1.36x greater in plots grazed for 10 min compared to ungrazed plots (Fig. A3.1.a). I assume, therefore, that the 1983 grazing level was equivalent to about 10 minutes of grazing by captive goslings under the regime described by Hik and Jefferies (1990), henceforth abbreviated as a grazing level of 10.

Fig. A3.1. Experimental data (symbols) and calculated equations (lines) for relationships between grazing and NAPP/leaf demography (a), between salinity and leaf demography (b), and between above-ground biomass and salinity (c). See text for details of equations.


a
TLB & NAPP
NAPP data
1983 demography data
1991 demography data
ASLB
ASLD
MSLB & MSLD
leaves/plant/day
NAPP after 60 days (g/m2)
Grazing level
b
MSLD
ASLB
MSLB
ASLD
1991 data
leaves/plant/day
salinity class
c
1991 data
salinity class
mid-July biomass (g/m2)

In 1983, demography of a major graminoid species, *Puccinellia phryganodes*, was studied in grazed and ungrazed swards (Bazely and Jefferies, 1989). Leaf birth and death rates on main and axillary shoots are known accurately. Similar demography data are also available for 1991 (Chapter 5). Leaf birth and death rates are similar for 1983 and 1991 ungrazed areas but not for grazed areas (Chapter 5). The latter may reflect increased grazing pressure and/or deleterious salinity effects. I assume that total leaf birth rate (sum of main and axillary shoot leaf birth rates) is linearly related to NAPP. Although NAPP will also be influenced by stem elongation, the latter is presumably directly related to leaf production as well. Total leaf birth rates (TLB) were 0.169 and 0.155 leaves/ plant/ day in 1983 and 1991, respectively, in ungrazed areas (mean=0.162) and NAPP was 46 g/m^2 in ungrazed areas in the captive gosling experiment. The quadratic curve fitted to the NAPP data (eq. 1) is multiplied by 0.162/46 to describe TLB as a function of grazing level (numbers rounded slightly for ease of calculations):

$$-13333(\text{TLB} - 0.274) = (\text{grazing level} - 40)^2 \qquad \text{[eq. 2]}$$

The measured 1983 grazed TLB is only slightly lower than the TLB predicted at a grazing level of 10 (see Fig. A3.1.a).

Total leaf birth rate is composed of the main shoot leaf birth rate (MSLB) and axillary shoot leaf birth rate (ASLB). In 1983, grazing caused a switch in resource allocation such that MSLB decreased and ASLB increased relative to ungrazed plants (the increase in ASLB exceeded the decrease in MSLB, so that TLB increased with grazing). As TLB increases to a maxima, MSLB is therefore predicted to gently decrease to a minima; beyond the TLB maxima (at a grazing level of 40), MSLB is predicted to increase, probably even more gently than it decreased because of below-ground resource depletion by heavy grazing. 1983 and 1991 ungrazed MSLB data and 1983 grazed datum were used to fit the quadratic MSLB curves (Fig a3.1.a):

if grazing level $<$ 40:

$$34999(\text{MSLB} - 0.0443) = (\text{grazing level} - 40)^2 \qquad \text{[eq. 3]}$$

if grazing level $\leq$ 40:

$$50000(\text{MSLB} - 0.0443) = (\text{grazing level} - 40)^2 \qquad \text{[eq. 4]}$$

The ASLB curve is generated simply by subtracting the MSLB curves from the TLB curve (1983 and 1991 data agree with its positioning):

$$\text{ASLB} = \text{TLB} - \text{MSLB} \qquad \text{[eq. 5]}$$

In most instances, the MSLD (main shoot leaf death rate) equals MSLB, irrespective of the grazing history (1983 and 1991 data). Therefore, it was assumed that MSLD equalled MSLB over all grazing levels.

$$\text{MSLD} = \text{MSLB} \qquad \text{[eq. 6]}$$

The last demography parameter, axillary shoot leaf death rate (ASLD), was represented by several equations, which caused the difference between ASLB and ASLD to decrease as grazing pressure increased:

if grazing level $<$ 15:

$$\text{ASLD} = 0.008\ (\text{grazing level}) + 0.02 \qquad \text{[eq. 7]}$$

if 15 $\leq$ grazing level $<$ 33:

$$\text{ASLD} = 0.02 + \frac{0.453\ (\text{grazing level})}{41.67 + \text{grazing level}} \qquad \text{[eq. 8]}$$

if grazing level $\geq$ 33:

$$\text{ASLD} = \text{ASLB} - 0.00033 \qquad \text{[eq. 9]}$$

Note that all the above demographic equations (eq. 2-9; Fig A3.1.a) use only 1983, not 1991, grazed plant data. It is assumed that 1983 represents a state dominated primarily by the NAPP-grazing feedback cycle; ie, salinity levels are low. The next two sets of equations will deal with factoring in this salinity component.

2) Effect of salinity on demography. In 1991, demographic data was collected for plants transplanted into areas of equal (low) density and similar grazing pressure but different soil salinity (Fig A3.1.b). The soil salinity (approximated by sodium concentration) can be grouped into three classes: with 1 the lowest salinity (0 to 2 g/L Na^+), 2 intermediate salinity (2 to 4 g/l Na^+) and 3 the highest (4 to 8 g/L Na^+). The factor by which MSLB, MSLD, ASLB, and ASLD are affected by salinity relative to salinity class 1 is as follows:

ASLB factor = -0.30 (salinity class) + 1.17 [eq. 10]

ASLD factor = -0.283 (salinity class) + 1.15 [eq. 11]

MSLB factor = 1 if salinity class <2 [eq. 12]

= else: -0.30(salinity class) + 1.6 [eq. 13]

MSLD factor = 1 if salinity class <2 [eq. 14]

= else: -0.15(salinity class) + 1.3 [eq. 15]

3) Effect of density on demography. Plants growing in areas of low density tend to have greater axillary shoot production than those in areas of higher density, but growth of main shoot leaves is similar (Chapter 5). Using demographic data for plants growing in low biomass (8300 plants/cm^2) and high biomass (45400 plants/cm^2) sites of similar salinity (salinity class 1), the amount by which ASLB and ASLD is increased in low density sites relative to high biomass (ie., high density) sites can be calculated as follows:

if density $>$ 8299 then:

ASLB increase $= 2.03 \times 10^{-6}$ (45400 - density) [eq. 16]

ASLD increase $= 7.68 \times 10^{-7}$ (45400 - density) [eq. 17]

if density $\leq$ 8299 then;

ASLB increase $= 0.0774$ [eq. 18]

ASLD increase $= 0.0293$ [eq. 19]

Note that since densities lower than 8300 plants/cm^2 (low biomass sites) were not examined, it is assumed that density has no further effect beyond this density, as suggested in Chapter 5 (discussion). It is also assumed that there is no density x salinity interaction.

4) Effect of biomass on salinity. The known biomass-salinity relationship (Chapter 4) was transformed into a biomass-salinity class relationship as follows. Sodium concentration in the soil-water of the demography sites (high biomass and low biomass) was measured on August 15, 1991 and in high biomass, low biomass, and bare sites was measured on August 31, 1991. Since high biomass sites had similar sodium concentrations in soil-water on August 15 and August 31 (mean of 1.57 and 1.42 g/L Na respectively), I assume that salinities on these two dates are comparable. The mean soil salinity for salinity class 1 is 1.6 g/L Na (Aug. 15), and for the high biomass category is 1.5 g/L Na (Aug. 31). The mean salinity for class 3 is 6.1 g/L Na, and for bare areas is 6.4 g/L Na. The mean salinity of class 2 was 2.9 g/L Na; the fit with August 31 low biomass areas, salinity of 4.0 g/L Na, is less satisfactory. Using the above comparisons, and mid-July biomass estimates of 57, 20, and 0 g/m^2 for high, low and bare areas respectively, the relationship between peak biomass and salinity class is calculated to be (Fig A3.1.c):

$$\text{salinity class} = 6.5\ ((\text{biomass} + 22)/14)^{-1.1} \quad \text{[eq. 20]}$$

5) Converting demography data to NAPP and mid-July biomass. As argued earlier, NAPP

should be directly related to total leaf births (leaf biomass loss is inconsequential to productivity):

Season-end NAPP = TLB (leaves/plant/d) * 70 d/season [eq. 21]
* density (plants/m^2) * g/leaf.

In 1983, NAPP and TLB is known for grazed and ungrazed areas, density of high biomass sites is assumed to be about 45400 plants/m^2 (Chapter 2), so it is then possible to solve for leaf weight ($1.62 * 10^{-4}$ g/leaf). Note that this value includes the piece of stem between each leaf and the previous one. This value is comparable a 1991 estimate of $4 * 10^{-4}$ g/leaf with stem.

Biomass is equal to leaf biomass produced minus that eaten or dead; ie, it is directly related to (TLB-TLD). Therefore, an initial equation might be:

biomass = (TLB-TLD) * 70 days * density [eq. 22]
* $1.62 * 10^{-4}$ g/leaf.

This, however, provides an end-of-season estimate of biomass, and what is needed is a mid-July estimate of biomass, which will be considerably higher. Also, there is some initial biomass before demography began which is unaccounted for. Both the above considerations are accounted for by multiplying the initial biomass equation (eq. x) by 5.34, a corrective value estimated with 1983 biomass and demography data.

biomass = (TLB-TLD) * 70 days * density [eq. 23]
* $1.62 * 10^{-4}$ g/leaf * 5.34

6) Within season model. The above relationships were combined in a simple model using Turbo Pascal (see next page). The steps are as follows. Grazing level is input, and demographic parameters (ASLB, ASLD, MSLB, MSLD, TLB, TLD) are calculated as in eq.

2-9. By multiplying by the appropriate equations (eq. 21 and 23), NAPP and biomass estimates are generated. Using this biomass estimate ("uncorrected biomass"), the salinity class can be estimated as described in eq. 20. ASLB, ASLD, MSLB, and MSLD are then reduced (or increased) by the appropriate factor to reflect salinity influence (eq. 10-15). Finally, the effect of density is accounted for by eq. 16-19. Thus new TLD and TLB values are generated, and from these new biomass and NAPP values can be estimated ("corrected biomass") using eq. 21 and 23.

Within season Turbo Pascal program

```
program season;

var
aslb,mslb,tlb,asld,msld,tld,napp,biomass,graze,salinity,density:        real;

begin

writeln('grazing pressure? (0 to 100)'); readln(graze);
writeln('density? (0 to 45400)'); readln(density);

if graze<40 then mslb:=0.0443+(sqr((graze-40)))/34999 else
        mslb:=0.0443+(sqr((graze-40)))/200000;
tlb:=0.274+(sqr((graze-40)))/-13333;
aslb:=tlb-mslb;
if graze<15 then asld:=0.008*(graze)+0.02;
if graze>35 then asld:=aslb-0.000327 else
asld:=0.02+(0.453*graze)/(41.67+graze);
msld:=mslb;
tld:=asld+msld;

napp:=tlb*density*70*0.000162;
biomass:=(tlb-tld)*density*70*0.000162*5.34;
writeln('initial biomass is ',biomass:4:1);
writeln('initial napp is ',napp:5:1);

salinity:=6.5*exp(-1.1*ln((biomass+22)/14));
aslb:=aslb*(1.17+(-0.30*salinity));
asld:=asld*(1.15+(-0.282*salinity));
if salinity>2 then mslb:=mslb*(1.6+(-0.3*salinity));
if salinity>2 then msld:=msld*(1.3+(-0.15*salinity));
if density>8299 then aslb:=aslb+0.00000203(45400-density) else
        aslb:=aslb+0.0774;
if density>8299 then asld:=asld+0.000000768(45400-density) else
        asld:=asld+0.0293;
biomass:=(aslb+mslb-asld-msld)*density*70*0.000162*5.34;
napp:=(aslb+mslb)*density*70*0.000162;

writeln('salinity is ',salinity:2:1);
writeln('corrected biomass is ',biomass:4:1);
writeln('corrected napp is ',napp:5:1);

end.
```

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